# CHAPTER 2: BIOGEOGRAPHY OF KWONGAN: ORIGINS, DIVERSITY, ENDEMISM AND VEGETATION PATTERNS

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## INTRODUCTION

BIOGEOGRAPHY IS THE SCIENCE OF patterns of distribution of organisms, and processes shaping these patterns. Geographic distribution of genes falls within the realm of biogeography and major progress in this direction enhanced the emergence of phylogeography (Avise, 2000). The study of patterns of distribution of plant clades (as defined by molecular phylogenetic studies) and the evolutionary processes underpinning these patterns has led to the establishment of phylogenetic geography: developing and testing sets of hypotheses and methodical approaches and tools. The phylogeography and to a small extent the geographic patterns of the distributions of plant clades in kwongan are discussed in chapter 3.

This book is about *plant* life; hence we could use the term *phyto*geography. However, we prefer the more general term, because of its wider use. Both flora and vegetation will be subject of our enquiry. Flora is defined as all plants co-occurring in a region and time period. Phenomena such as species numbers, recent and past spatial distribution of species, geo-elements, patterning and formation of centres of endemism, role of macro-ecological and macro-evolutionary processes are typical biogeographical subjects focusing on flora. On the other hand, vegetation is the subject of vegetation science, in the past referred to also as 'plant geography'. Co-occurring plants form plant communities, steered by environmental filters and assembly rules (Wilson, 1999; Grime & Pierce, 2012), at various spatial and temporal levels of complexity; the plant communities (and their high-order complexes) form the vegetation of the region.

Both flora and vegetation are results of a plethora of environmental, historical and evolutionary drivers. In this chapter we pay much attention to describing the flora and vegetation patterns, and also to drivers and the underpinning processes that presumably shape those patterns. Floristic patterns and processes are, by definition, of broad spatial and long temporal scales. The vegetation patterns, on the other hand cover a large spectrum of spatial scales, ranging from microhabitats supporting micro-assemblages to biomes supporting (sub)continental biotic assemblages. The ecological assembly processes (operating along ecological time scales) are possibly those responsible for major current vegetation patterns. Yet, the processes operating along evolutionary time scales (thousands to tens of millions of years) do leave their mark on vegetation, especially in old landscapes. We deal with this phenomenon when analysing the ecological-evolutionary theory of old, stable landscapes (Hopper, 2009; Mucina & Wardell-Johnson, 2011). The enquiry into patterns of alpha and beta diversity in vegetation will serve as a bridge to understand the richness of the flora on (supra)regional levels, uniting the concepts of biogeography and vegetation science.

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Flora is structured in space and its complexity and variability allows creation of spatially explicit concepts such as floristic regions, hotspots, centres of endemism (Takhtajan, 1986; Myers *et al.*, 2000; Hopper & Gioia, 2004). Vegetation is a supra-organismic concept, because of its spatially and temporally extremely complex phenomena; its study commands simplification by defining concepts such as plant community, vegetation series, formation, biome, as well as conceptual models such as various vegetation classification systems. This space of building of spatially explicit conceptual frameworks such as classifications is where biogeography and vegetation science meet. In this chapter we devote attention to this issue and discuss the position of plant life on Swanland sandplains in terms of both biogeographic and vegetation classifications.

The sandy plains of south-western Australia are home to unique flora and vegetation. Here we deal with plant life in kwongan (Beard, 1976a), a vegetation type typical of ancient landscapes of Western Australia, and finding its regional counterparts in heathlands of South Australia, western Victoria and south-western New South Wales and the wallum of the coastal seaboards of the Australian East Coast.

We choose to delimit kwongan in rather general and practical terms, embracing not only so typical proteoid- and myrtle-dominated scrub-heath and heath, but also *Banksia* woodlands, heath-like scrub of temporary wet depressions (heath swamp, non-proteoid thickets spatially (and ecologically) associated with the kwongan proper), and the low wind-pruned scrub of steep coastal slopes and cliff headlands. In this shape the concept of kwongan experienced an important conceptual expansion when compared with original delimitation offered by Beard (1976). Kwongan, the biological flagship of the Southwest Australian Floristic Region (SWAFR: Diels, 1906; Takhtajan, 1986; Hopper, 1979), will be the biogeographic theatre of this chapter. Yet understanding how it came about, where it is found, how complex it is, and why, must be understood in the context of other vegetation types of the region, including the wet and dry forests, temperate eucalypt woodlands, mallee, freshwater and saline as well as permanent and temporary wetlands and the coastal vegetation. Therefore some of the deliberations below would reach beyond the kwongan itself and discuss the patterns of SWAFR.

## ORIGINS OF PLANT LIFE IN KWONGAN

### Palaeobotany of the SWAFR

South-western Australia is a biodiversity hotspot for plant species, and the vegetation of the kwongan is a large part of this. How did this come about? The detailed answer is unknown since the evidence must come from the fossil record that is fragmentary at best. The single most important reason for this is the discontinuous nature of the geological record, as any geological map of Western Australia shows. Stated simply, the geology of Western Australia has abundant ancient rocks of the Proterozoic, which is long before the time of flowering plants. There are scattered outcrops of various ages in the region, but these are usually devoid of well-preserved fossils. Fortunately, there are some records of Tertiary and Quaternary age with well-preserved fossils (see below); together, these can be assembled to provide a workable hypothesis of how the biodiversity of the kwongan and the vegetation of the southwest came about.

Plant macrofossils, pollen and spores in sediments are the primary data in reconstructing past vegetation. These need to be in a well-dated context, so that the history can be pieced together. An

important element in the story is to understand how the flora developed in relation to plate tectonic movement and the resulting evolution of the climate. Australia separated from Gondwana around 50 million years ago (Ma). Just before this occurred, the Australian flora had strong affinities with other elements of Gondwana in being dominated by conifers, ferns and rainforest angiosperms. The Australian fragment of Gondwana then began a slow drift at a rate of 7–8 cm/yr from high southern latitudes to the mid latitude position it occupies today. This shifted Australia's position from a climate dominated by moisture driven by the southern westerlies to one where the subtropical high dominated. This was the most significant cause for the development of aridity, which began in the north and eventually reached all the way to the Nullarbor, while the far north drifted into the tropics and came under the influence of a monsoon climate. Separation and aridification were fundamental in the development of highly endemic uniquely-adapted flora. In addition, the long weathering and lack of volcanic and other land renewal processes resulted in ancient landscapes, which were highly weathered and leached, producing low-nutrient soils and the climate was conducive to a high fire frequency regime.

The geological record shows that south-western Australia separated from Gondwana about 5 Ma earlier than the southeast (*e.g.*, Hill, 1994; Clarke *et al.*, 2003), and the increasing aridity gradually reduced the southwest to become an 'island' of isolated sub-humid to moist climate (Bowler, 1976; Zheng *et al.*, 1998). Eocene lignites near Bremer Bay and the Eucla Basin show that the vegetation still contained some moisture-dependent taxa such as ferns, podocarps, *Agathis* and *Nothofagus* (Milne, 1998; Clarke *et al.*, 2003). At that time, however, the vegetation already had a high Proteaceae, Myrtaceae and Casuarinaceae component. These probably had rainforest ancestors (Hill, 1994). The West Dale formation near Perth is of mid-Eocene to Oligocene age (45–25 Ma) and Myrtaceae and Proteaceae were abundant, and sclerophylly was a feature of the vegetation. Various *Acacia* species were present as were low numbers of Asteraceae. Together these suggest the vegetation included many taxa suited to dry or seasonally-dry conditions. Seasonality was probably a prominent feature of the climate by this time.

The Pliocene (5.3–2.59 Ma) is regarded as a relatively warm and wet period, at least in its earlier days, with sea levels significantly higher than in the Pleistocene that followed. The Northern Sandplains near Dandaragan had a meteor impact of probable Miocene age that formed a large diameter crater called Yallalie. This was gradually in-filled and between 3.6 Ma and 2.5 Ma contained a lake. The sediments from this period contain an excellently preserved pollen and spore record, and in some cases macrofossils (Dodson & Ramrath, 2001; Dodson & Macphail, 2004). Today the site is buried under a 65 m sand sheet. The pollen and spores show that all the main elements of the kwongan were present, including Ericaceae, *Melaleuca*, *Leptospermum*, *Grevillea*, *Hakea*, *Banksia*, *Eucalyptus*, *Corymbia* and *Acacia*. There still was a small component of moisture-loving components such as podocarps, *Araucaria* and a diverse group of ferns. Charcoal is present in most of the samples investigated, and in parts of the record with apparently annual layers of deposition it is possible to estimate the return period of local fires, at somewhere between 8–14 years (Atahan *et al.*, 2004). This frequency is not strikingly dissimilar to the present day. Since this is well before humans were in Australia, this is an indication of the natural fire regime at the time. There were no extinctions of moisture-loving species apparently associated with fire. Finally, the Yallalie record shows several periods of aridity where halophytes indicate that salinisation also took place (Dodson & Lu, 2005). Each of these shows a reversal to low-salinity conditions, indicating that in the right circumstances salinity can be mitigated naturally.

The Quaternary, approximately the last 2.6 Ma, showed great swings in global climate from glacials to interglacials and changes of over 100 m in sea level as ice sheets waxed and waned. The rapidity of these climate shifts seems to be unparalleled in the geological record. In most temperate regions, this caused major shifts in ice cover and the distribution of species and vegetation cover. In south-eastern Australia areas now heavily wooded became steppe-like, with forest patches surviving in refugia. There are not many records for south-western Australia, but the pattern may have been different according to a record from Bibra Lake in Perth (Pickett *et al.*, 2004). The sediment there goes through the last global glacial maximum at about 21 ka, and the pollen record shows the area was wooded throughout. If this is general, then the impact of the last glacial may not have been particularly severe in the southwest. Or perhaps the great diversity itself provided many pre-adapted species to cope with whatever the environment threw at them? There are several Holocene to part Holocene pollen records from south-western Australia (*e.g.*, Dodson & Lu, 2000). The Holocene is the present interglacial. The records are remarkable in that they do not show large degrees of vegetation change at the generic or vegetation formation level. Interestingly, that other great southern hemisphere centre of biodiversity, the Cape Province of South Africa, also has late Pleistocene and Holocene records showing little change in vegetation (*e.g.*, Meadows & Baxter, 2001).

## Drivers of plant diversity: cradle or museum?

Identifying the drivers of evolutionary change underpinning the high species richness and staggering levels of local and regional endemism making the SWAFR a global biodiversity hotspot has intrigued many scientists since these phenomena have been revealed (Beard *et al.*, 2000; Hopper, 1979, 2009; Hopper & Gioia, 2004; Mucina & Wardell-Johnson 2011; Crisp & Cook, 2013). Here we provide a scenario listing the putative drivers from the global to continental and finally to regional spatial scale (Table 1).

At a global scale, the Australian flora (and the SWAFR flora alike) has experienced several global aridisation events (late Eocene/Oligocene, post Mid-Miocene and Pliocene-Pleistocene), due to different planetary dynamics. At the same scale, the flora of Australia should have experienced serious changes due to Gondwanan break-up, which started around 120 Ma and culminated in the isolation of the Australian continent (nearly in the shape as we know it today) about 33 Ma. The break-up might have caused large-scale volcanic events (Decan and Karoo volcanism) that have had a global impact on the climate. The K/T bolite impact probably had less impact on the flora than on animal life, yet it should not be dismissed (for references see Mucina & Wardell-Johnson, 2011; Crisp & Cook, 2013).

At the continental spatial scale, the insulation of Australia associated with the opening of the Tasman passage and hence the emergence of Circumantarctic Circulation is considered both as a major tectonic, but also an evolutionarily relevant event shaping the arid nature of the Australian flora. The influence of the growing importance of the Antarctic vortex was exacerbated by the northwards movement of the continent (Beard, 1977), leading eventually to establishment and expansion of the arid center of Australia and assembly of the arid flora (Byrne *et al.*, 2008), eventually isolating SWAFR from the mesic/wet East Coast (Crisp *et al.*, 2004) by aridisation of the Nullarbor Plain.

Based on his research in SWAFR and several authoritative reviews (Hopper, 1979; 1992; Hopper & Gioia, 2004), Hopper (2009) recognised landscape age, climate buffering, and soil nutrient status as descriptors for an evolutionarily important continuum between old, climatically-buffered landscapes characterised by low soil fertility (OCBILs) and young, often disturbed landscapes characterised by fertile

soils (YODFEL). Mucina & Wardell-Johnson (2011) redefined Hopper's climate buffering as a dimension of climate stability, identifying the declining soil nutrient status as a function of landscape age, and recognising fire regime predictability as a large-scale, long-term evolutionarily important dimension – drivers of the evolutionary change at the regional (SWAFR) scale (Fig. 1). In so doing, they also constructed a globally relevant, qualitative template (OSL: Old Stable Landscapes) to enable the testing of evolutionary-ecological hypotheses concerning biodiversity (*e.g.*, species diversity, diversity gradients, endemism, speciation and extinction rates, persistence of old lineages, refugial phenomena) at scales beyond the region (Mucina & Wardell-Johnson, 2011).

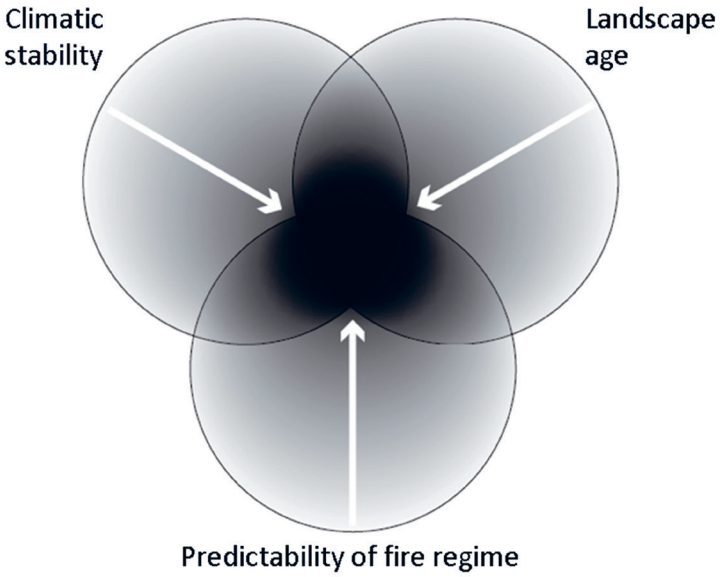


Figure 1. A model of the Old Stable Landscape (OSL) system relying on the three templates representing dimensions of landscape age (decreasing soil nutrient concentrations), climate stability (predictability), and predictability of fire regime. The arrows indicate the increased probability of the occurrence of an OSL (after Mucina & Wardell-Johnson, 2011).

In sync with the latest review of the processes (and the associated drivers) of the flora assembly of the Australian continent (Crisp & Cook, 2013), we concur that the flora of SWAFR is a subset of the Australian flora, which, in turn, is considered to be a 'modified sample of the global flora, with some distinctive characteristics resulting from idiosyncratic events (rise to dominance by particular flammable, sclerophyll lineages) early in its existence as an island', to cite the conclusive statement of Crisp & Cooks' analysis.

At the population and community level the putative drivers of the evolutionary processes such as speciation, extinction and migrations are probably of the same quality and magnitude as recognised in the sister OSL – the Cape of South Africa (Rebelo *et al.*, 2006). These would include the habitat and population fragmentation through recurrent disturbance (fire in the first place), which in the presence of fine-scale soil (and geology) mosaics and in combination with limited propagule dispersal could lead to adaptive radiations (see also Crisp & Cook, 2013). The insect–plant interactions (especially pollination and propagule dispersal) could have played an equally important role at the community level by producing novel ecologically positive interactions (mutualisms), which could either drive or enhance the adaptive radiation underpinned by soil mosaic (Van der Niet & Johnson, 2009; Johnson 2010; chapter 7).

The mechanisms underpinning the speciation at the cell and molecular levels are documented by examples in chapter 3.

| SCALE | DRIVER | BIOTIC SCALE | SCALE OF IMPACT | TIME (WHEN?) | PROCESS (HOW IT HAPPENS?) |
|---|---|---|---|---|---|
| Glob | Gondwana break-up | biosphere | global scene | ever since creation of crust | plate tectonics |
| Glob | Opening of Tasman passage | supra-biome | circum-continental dynamics | | plate tectonics |
| Glob | Australian tectonic drift northwards | supra-biome | circum-continental dynamics | 35 Ma till today? | plate tectonics |
| Glob | Global changes of sea levels | supra-biome | circum-continental dynamics | recurrent | thawing and growing of ice shields |
| Glob | Plio-Pleistocene climate fluctuations | supra-biome | circum-continental dynamics | since app. 5 Ma | Milankovich forcings |
| Glob | Large-scale volcanic activity | biosphere | global scene | | coordinated volcanic activity in different locations on the planet (e.g. Dekan Plateau volcanism, Jurrasic post-spli volanism in southern Africa), leading to abrupt climate change |
| Glob | Bolite impacts | biosphere | global and supra-biome | rare | impact of large bolites (asteroids, meteorites, cometes) leading to chain of large-scale devastating disruptions (earthquakes, tsunamis, temporary 'nuclear' winters, poisoning of athmosphere and waters) |
| Cont | Establishment of Australian arid zone | biome | circum-continental dynamics | 35 Ma till today? | Australian tectonic drift northwards |
| Cont | Emergence of altitudinal differences | biome | intra-continental dynamics | 10–8 to 10–6 Ma | erosion of softer rocks exposing hard-rock formations; may lead to exposure of new geology and formation of habitat mosaics |
| Cont | Dissection of continuous surfaces | biome | intra-continental dynamics | 10–8 to 10–6 Ma | uneven erosion along faults and of soft rocky insertions |
| Cont | Flattening of the landscapes | biome | intra-continental dynamics | 10–8 to 10–6 Ma | prevalence of erosion over tectonic uplift due to lack of the latter |
| Reg | Nutrient impoverishment | biome | supra-regional dynamics/ OSL element | since last 600 yrs in WA | slow, yet steady eluviation of nutrients from regolith due to lack of soil rejuvenation processes |
| Reg | Fire regime | biome | supra-regional dynamics/ OSL element | since Cretaceous, enhanced at the end of Eocene and in Oligocene) and then since Mid-Miocene | change of fire sensitivity of the landscapes as resiult of increased aridity, onset of climatic (rainfall) seasonality, associate with putative potivove feedback enhancing fire frequency throiugh emerging fire-enhancing traits |
| Reg | Climate predictability | biome | supra-regional dynamics/ OSL element | in SWAFR since emergence and establishment of seasonality (edn of Miocene? | long-term persistence (over evolutionary time scales) of established climatic regimes (seasonality in SWAFR) |
| Reg | Animal migrations | sub-biome | intra-continental dynamics | since emergence of climatic seasonality (?) | alnd animal and bird migrations are response to emergence of climatic seasonality (?) forcing animals to seek food in less impacted regions |
| Reg | Formation of habitat mosaics | sub-biome | regional dynamics | ever since | habitat complexes (spatially close) can emerge through erosion-sedimentation cycles, flooding-draining cycles, distubance by large-scale fires and animal grazing *etc.* |

| EVOLUTIONARY CONSEQUENCE | NOTE |
|---|---|
| first step towards insulation of Australia | |
| increased insulation of Australia; formation of Circum-Antarctic Circulation leading to | |
| change of vegetation zonation in response to changing position of the continent in relation to the Equator | |
| formation and obliteration of coastal habitats; insulation and rejoining of land masses | |
| | possibly one of the most globally important 'modern' evolutionary driver |
| short term: obliteration of habitats pushing many species (and communities towards extinction; long term: creation of new habitats characterised by nutrient-rich soils | |
| short term: obliteration of habitats and much of the biota (to the etent of Mass Extinction); long term: change of competitive relationships in biotic communities, enhancing chances of the survivors to take over and evolve | |
| insulation of south-western WA from East Coast wet regions | |
| emergence of insular habitats such as bornhards (granite outcrops) and inselberg ranges (Stirling Range) | |
| emergence of tafelbergs, scarps and valleys such as Mt Lesueur and XXX N of Geraldton; general articulation of landscapes | |
| creation of plateau landscapes; smoothing of elevation gradients and creation of fin-scale shallow gradients; may lead to exposure of new geology and formation of habitat mosaics | |
| trait filtering through increasing leaching of P and N from soils leading to gradual creation of new habitats (and biomes) as well as emergence of ecological innovations and creation of new mutualistic partnerships | extremely slowly disruptive but also creative force creating major peinobiomes of the World |
| selection for fire-tolerance and enhancement of 'borrowed traits' (abaptation), associated putatively with fire-dependent traits enhancing the importance of fire as major regeneration force; disruption of large plant populations leading to temporary (or permanent?) isolation | both-long term (along evolutionary scale) both disruptive and creative force maintaining fire-prone landscapes |
| predictable climatic regime associated with slowing of extinction rates (museum effect) | main stabilising force on the biome-level creating long-term evolutionary 'refugia' |
| enhanced possibility of (repeated) assisted long dispersal of plants | |
| | |

Table 1. Global, continental and regional tectonic, geological, climatic an disturbance drivers as evolutionary creative and destructive forces, relevant to the evolution and assembly of flora in the SWAFR.

Table 2. Top 20 families and genera (in terms of species number) in the SWAFR and in the Core Cape Flora (incl. the traditional Cape Floristic Region and some embedded regions of the Succulent Karoo; redefined by Manning & Goldblatt, 2013). The blue highlighted families are the Great Five, while the bold highlighted genera are preferably occurring in kwongan (SWAFR) heath or fynbos shrublands (CFR). Data were sourced from FloraBase, accessed on 10 October 2013. NS: number of species.

| FAMILY/SWAFR | NS | GENUS/ SWAFR | NS | | FAMILY/CFR | NS | GENUS/CFR | NS | |
|---|---|---|---|---|---|---|---|---|---|
| Myrtaceae | 1268 | *Acacia* | 438 | **Fabaceae** | Asteraceae | 1077 | ***Erica*** | 680 | Ericaceae |
| Fabaceae | 1026 | *Eucalyptus* | 313 | **Myrtaceae** | Fabaceae | 764 | ***Aspalathus*** | 273 | Fabaceae |
| Proteaceae | 765 | ***Leucopogon*** | 209 | **Myrtaceae** | Iridaceae | 758 | ***Restio*** | 163 | Restionaceae |
| Orchidaceae | 382 | ***Stylidium*** | 208 | **Stylidiaceae** | Ericaceae | 680 | ***Agathosma*** | 163 | Rutaceae |
| Ericaceae | 371 | ***Grevillea*** | 195 | **Proteaceae** | Aizoaceae | 624 | *Pelargonium* | 150 | Geraniaceae |
| Asteraceae | 290 | ***Melaleuca*** | 182 | **Myrtaceae** | Scrophulariaceae | 419 | ***Phylica*** | 132 | Rhamnaceae |
| Cyperaceae | 250 | ***Banksia*** | 156 | Proteaceae | Restionaceae | 342 | ***Cliffortia*** | 125 | Rosaceae |
| Stylidiaceae | 217 | ***Caladenia*** | 146 | Orchidaceae | Proteaceae | 333 | *Oxalis* | 122 | Oxalidaceae |
| Goodeniaceae | 204 | ***Gastrolobium*** | 111 | Fabaceae | Rutaceae | 295 | *Moraea* | 122 | Iridaceae |
| Malvaceae | 184 | ***Hibbertia*** | 104 | Dilleniaceae | Orchidaceae | 234 | *Senecio* | 114 | Asteraceae |
| Lamiaceae | 173 | ***Hakea*** | 100 | Proteaceae | Poaceae | 217 | ***Muraltia*** | 109 | Polygalaceae |
| Poaceae | 171 | ***Baeckea*** | 100 | Myrtaceae | Cyperaceae | 207 | *Gladiolus* | 108 | Iridaceae |
| Amaranthaceae | 135 | ***Verticordia*** | 96 | Myrtaceae | Hyacinthaceae | 200 | ***Selago*** | 100 | Scrophulariaceae |
| Rutaceae | 133 | ***Daviesia*** | 91 | Fabaceae | Asphodelaceae | 170 | ***Disa*** | 100 | Orchidaceae |
| Restionaceae | 110 | ***Drosera*** | 91 | Droseraceae | Geraniaceae | 158 | *Crassula* | 97 | Crassulaceae |
| Asparagaceae | 109 | *Lepidosperma* | 79 | Cyperaceae | Polygalaceae | 142 | *Geissorhiza* | 94 | Iridaceae |
| Dilleniaceae | 104 | *Schoenus* | 78 | Cyperaceae | Apiaceae | 138 | *Ruschia* | 87 | Aizoaceae |
| Rhamnaceae | 96 | *Eremophila* | 72 | Myoporaceae | Rhamnaceae | 138 | ***Thesium*** | 86 | Thesiaceae |
| Droseraceae | 92 | ***Synaphea*** | 70 | Proteaceae | Rosaceae | 131 | ***Leucadendron*** | 84 | Proteaceae |
| Scrophulariaceae | 85 | ***Darwinia*** | 63 | Myrtaceae | Crassulaceae | 130 | *Helichrysum* | 81 | Asteraceae |
| Total NS | 7239 | | | | | 9383 | | | |
| Endemism | 79% | | | | | 68% | | | |

## FLORISTIC BIOGEOGRAPHIC PATTERNS

The kwongan flora is comparable with few other floras in the world in terms of composition, richness and diversity. Here, we draw a comparison with the biogeographic (taxonomic) patterns with the Cape (defined as the Cape Floristic Region, CFR and called 'Core Cape Flora' by Manning & Goldblatt, 2012) and not the Greater Capensis *sensu* Born *et al.* (2006) because of its striking similarities in geographic position (similar latitudes on Southern Hemisphere, ecological fabric and ancient Gondwanan links reflecting commonalities in evolutionary history, of the respective floras (see Hopper, 2009: OCBIL; Mucina & Wardell-Johnson, 2011: OSL)). The census of taxa for the SWAFR in this section relies on FloraBase (http://florabase.dpaw.wa.gov.au/) data as accessed on 10 October 2013.

## FLORISTIC RICHNESS AND ENDEMISM

### Taxonomic patterns

A floristic comparison between the SWAFR and CFR (Table 2) shows that they are strikingly similar in their dominant families: eleven families are shared in the top 20 lists for the two regions, while four of the top five families in the SWAFR and three of the top five in the CFR are shared in the top 20. In the

SWAFR, the five most species-rich families are (in descending order): Myrtaceae, Fabaceae, Proteaceae, Orchidaceae and Ericaceae (Table 2). The majority of species in all five families possess special eco-morphological adaptations to oligotrophy (ectomycorrhizas, nitrogen-fixing bacteria, proteoid roots, orchidaceous fungal associations, and ericoid mycorrhizas, respectively). The high prevalence of nutrient-impoverished soils in the SWAFR provides a likely explanation for the adaptive significance and evolutionary importance of these adaptations to low nutrients in this area (Hopper, 2009; Lambers *et al.*, 2010; Mucina & Wardell-Johnson, 2011; chapter 4).

In comparison, the CFR top five families are: Asteraceae, Fabaceae, Iridaceae, Ericaceae and Aizoaceae. While two of these families (Fabaceae and Ericaceae) have adaptations to nutrient-impoverished soils, such adaptation are not known for the other three (Asteraceae, Iridaceae and Aizoaceae). Note that the CFR in the latest spatial redefinitions (Manning & Goldblatt, 2012) also contains significant areas of karoo semi-desert succulent shrubland vegetation (Robertson Karoo, Little Karoo), perhaps accounting for the high species diversity of Aizoaceae. However, the SWAFR as delimited also contains significant areas of woodlands and forests on heaver, less nutrient-impoverished soils, so the comparisons between the areas remains valid in the broadest sense.

Similarly, the broad structuring of phylogenetic diversity is similar between the regions. In both regions the average generic richness (the number of genera per family) and average species richness (the number of species per genus) are similar, but only if the single outlying genus and family (*Erica* in the Ericaceae) is removed. The situation with respect to *Erica* in the CFR – a single large genus and the only regional representative in the family – has no analogue in the SWAFR. The nearest Australian equivalents are the genera *Eucalyptus*, contributing more than 300 species, and *Acacia* with 431; however, these are unusually species-rich genera in genus-rich families rather than striking outliers like the Ericaceae in the CFR.

Myrtaceae and Proteaceae (Figs 2 and 3) are characteristic families of the kwongan, and are diverse in both genus and species numbers and in morphology. Nine of the 20 most species-rich genera belong to these two families (Proteaceae: 4; Myrtaceae: 5, although these figures will change with likely taxonomic changes particularly involving mergers or splits in *Grevillea*, *Hakea*, *Baeckea*, *Melaleuca*, *Verticordia* and *Darwinia*). Proteaceae has a similar genus and species richness in the SWAFR and CFR, while Myrtaceae is not well represented in the latter.

Within the SWAFR, Fabaceae (Fig. 4) is the most species-rich genus, largely because of a major contribution from *Acacia*. *Acacia* is not well represented in the kwongan itself, but is often a dominant component of the closely related wodjil thickets. More common in kwongan are the Australasian endemic sister tribes Mirbelieae and Bossiaeeae (both Papilionoideae), which have their highest Australian diversity within SWAFR and contain several genera with more than 50 species each (*Daviesia*: 91; *Jacksonia*: 74; *Pultenaea*: 104; *Gastrolobium*: 109; *Bossiaea*: *c.* 60).

The Ericaceae, as noted above, are a striking contrast between the SWAFR and the CFR. Represented in Australia by the subfamily Styphelioideae (previously treated as the family Epacridaceae), it is both species- and genus-diverse in the SWAFR, and is particularly diverse in kwongan. Subfamily Stypehelioideae has a principally southern-hemisphere distribution, being found in Australia, New Zealand, adjacent areas of south-east Asia and in southern South America (but not South Africa). By contrast, in the CFR, Ericaceae is represented by the single large genus *Erica*, a genus with species native to other regions in Africa, Madagascar, the Mediterranean and Europe. It is currently unclear whether

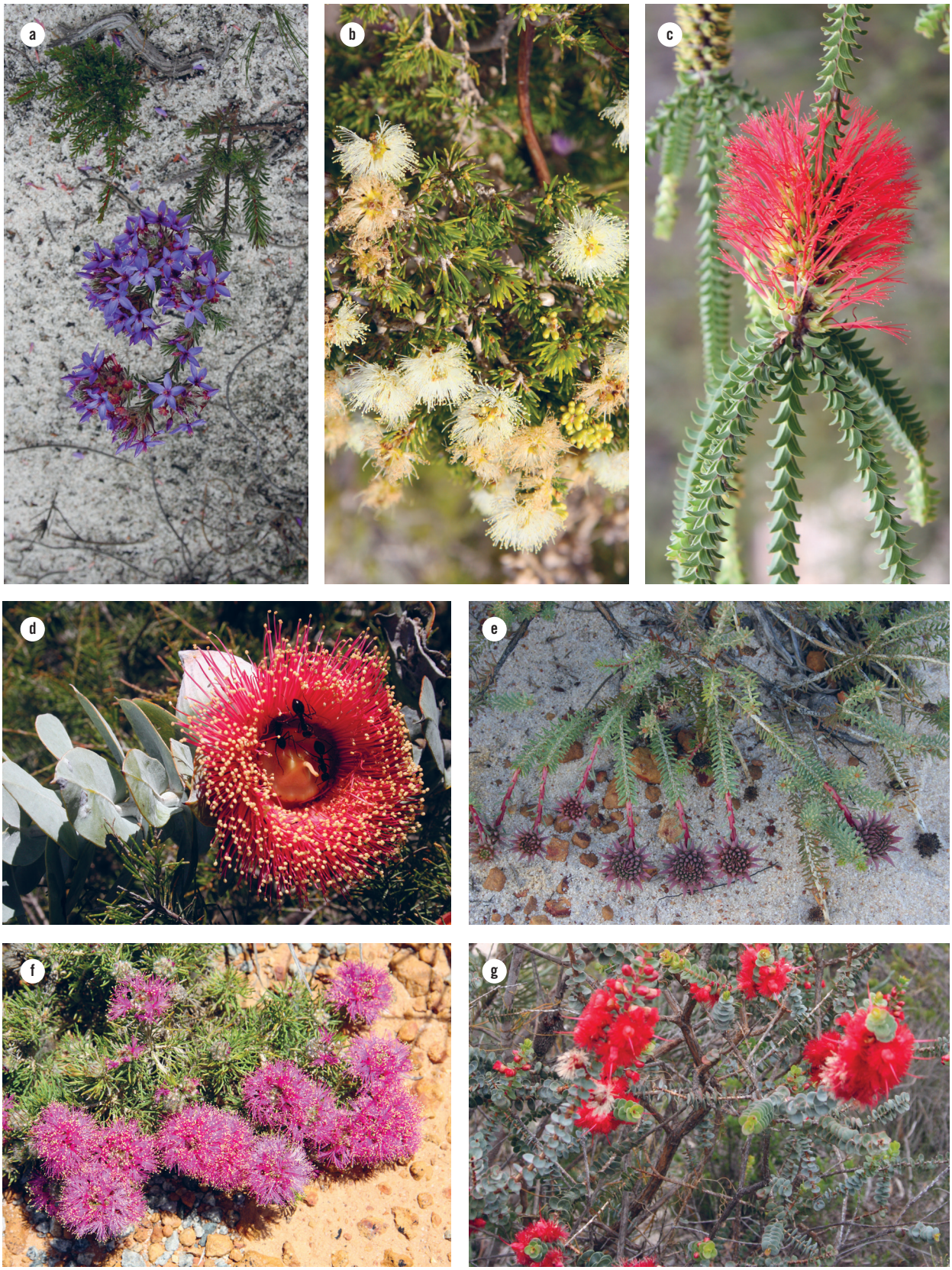


Figure 2. Representatives of the Myrtaceae typical for kwongan heath. (a) *Calytrix sapphirina*, (b) *Melaleuca acerosa*, (c) *Beaufortia decussata*, (d) *Eucalyptus macrocarpa* subsp. *macrocarpa*, (e) *Darwinia virescens*, (f) *Eremaea cf. fimbriata*, (g) *Verticordia grandis*. Photos: Ladislav Mucina.

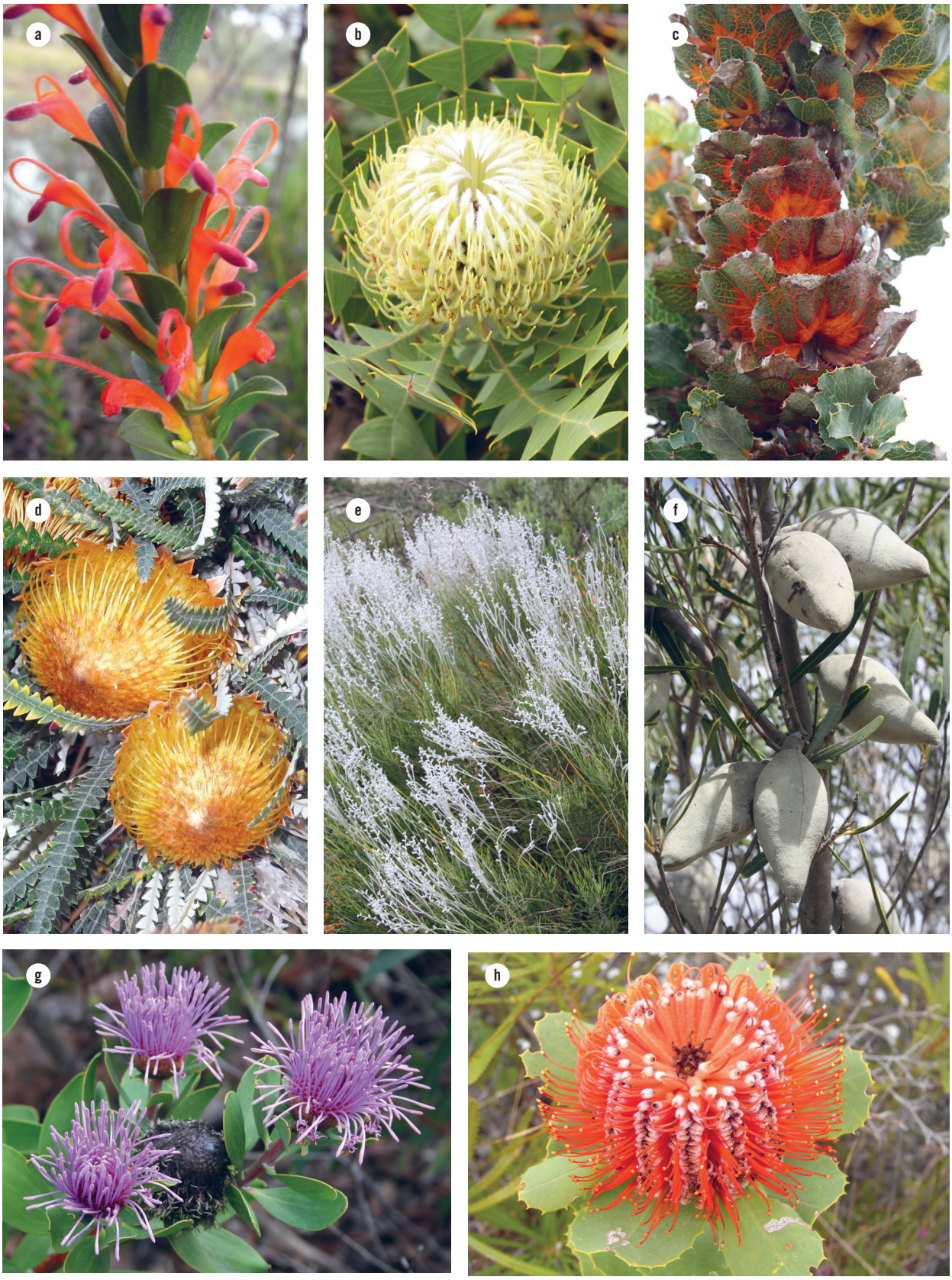


Figure 3. Representatives of the Proteaceae typical for kwongan heath. (a) *Adenanthos barbiger*, (b) *Banksia baxteri*, (c) *Hakea victoria*, (d) *Banksia formosa*, (e) *Conospermum stoechadis*, (f) *Xylomelum angustifolium*, (g) *Isopogon latifolius*, (h) *Banksia coccinea*. Photos: Ladislav Mucina.

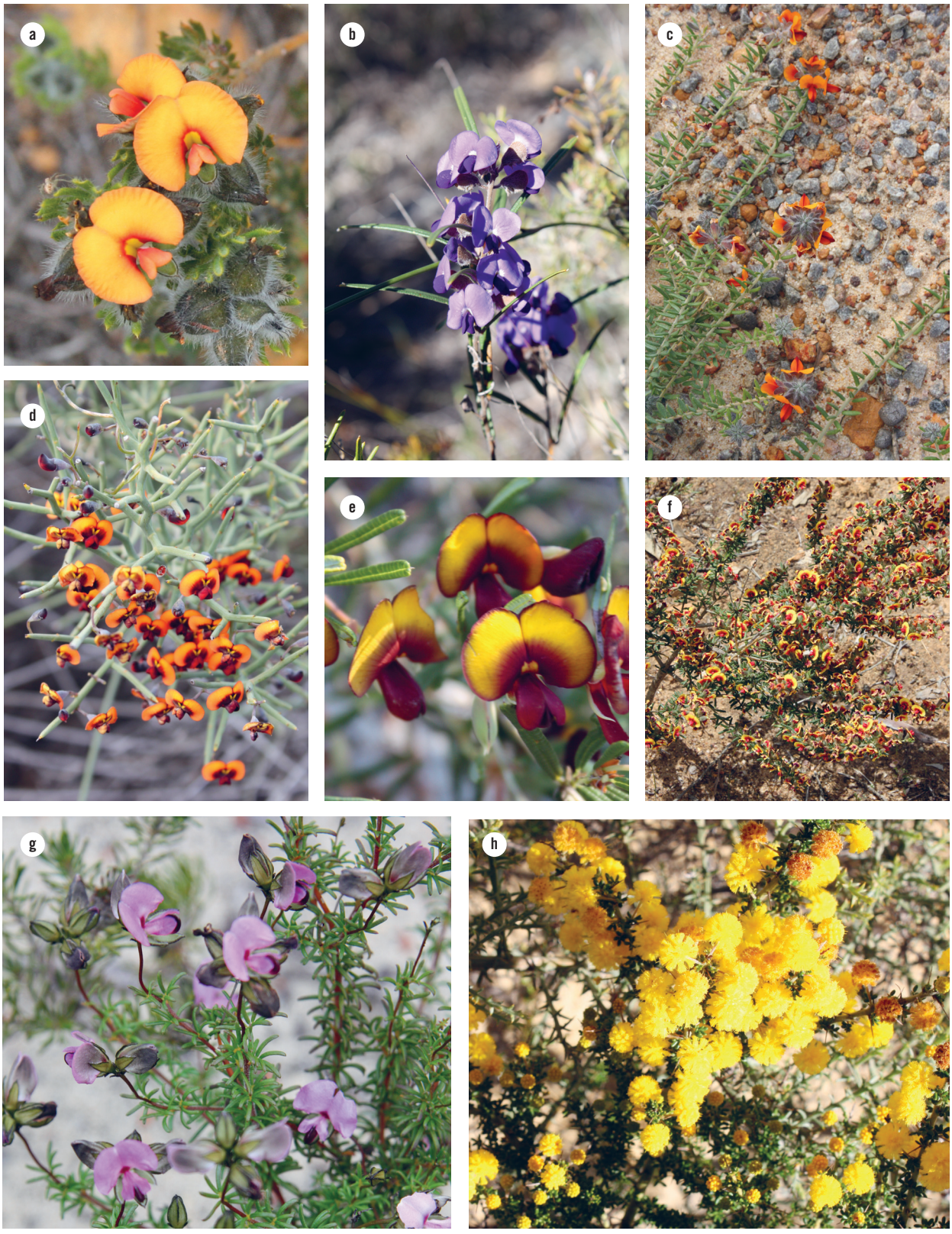


Figure 4. Representatives of the Fabaceae typical to kwongan heath. (a) *Gompholobium preissii*, (b) *Hovea trisperma*, (c) *Urodon dasyphyllus*, (d) *Daviesia divaricata*, (e) *Bossiaea eriocarpa*, (f) *Gompholobium shuttleworthii*, (g) *Mirbelia spinosa*, (h) *Acacia lasiocarpa* var. *lasiocarpa*. Photos: Ladislav Mucina.

this remarkable pattern represents recent dispersal into and radiation within the CFR, or a recent rapid radiation of an older lineage as conditions became favourable to it. In both cases, Ericaceae species are characteristic of oligotrophic soils in kwongan and fynbos.

Asteraceae is ranked the sixth-largest family in SWAFR; here we comment on its importance mainly because it is the most genus and species diverse family in the CFR. In neither region is the family well represented on nutrient-impoverished soils, preferring the somewhat richer soils of the intercalated herb-rich woodlands and granite outcrops in the SWAFR, and the herb-rich renosterveld shrublands of the CFR. Interestingly, in both CFR and SWAFR, Gnaphalieae is the most species-rich tribe of Asteraceae.

Other important families in kwongan include Haemodoraceae, Casuarinaceae, Goodeniaceae, Rutaceae, Hemerocallidaceae. (Figs 5A, B).

## Taxonomic patterns of endemism

In both the SWAFR and the CFR, endemic families and genera are important floristic elements, though in neither case do they dominate the vegetation or exhibit very high richness values. However, this hides a striking difference: only two of the 20 most species-rich genera in the SWAFR (*Synaphea* and *Darwinia*) are endemic or near-endemic to it, and none of the five most species-rich genera in the SWAFR are endemic; indeed, all are widespread in Australia. By contrast, in the CFR, many genera, including many in the top 20, are near-endemics (Manning & Goldblatt, 2012).

Taking into account smaller families, the SWAFR exceeds the CFR in numbers of endemic families (Figs 6A, B). Many of these are phylogenetically interesting, particularly including a number of small endemic families that are sister to large, cosmopolitan ones. Examples include Dasypogonaceae (possibly sister to Arecaceae) and Ecdeiocoleaceae (sister to Poaceae). Other examples of endemic families that are phylogenetically somewhat isolated are Anarthriaceae, Cephalotaceae, Emblingiaceae and Eremosynaceae (the latter has recently been placed tentatively in Escalloniaceae, but is somewhat isolated within that family). It is usually assumed that these are old relics; however this has rarely been tested and is often untestable in the absence of a good fossil record. All are found in kwongan shrublands.

## Geographic patterns of endemism

The SWAFR has a relatively high endemism on continental and global scales (Meyers *et al.*, 2000), although Hopper & Gioia (2004) note that species endemism estimates have been declining steadily since the 1990s (*e.g.,* 80% in Marchant, 1991; 53% in Beard *et al.*, 2000). An estimate based on specimen records at the WA Herbarium gives a current figure of 58% of plant species in the SWAFR as endemic. Given that a number of principally non-kwongan SWAFR families have relatively low levels of species endemism (*e.g.*, Asteraceae), the figure for kwongan is likely to be higher than the overall SWAFR figure.

An interesting distribution pattern has been revealed in some iconic Australian (sub)endemic families such as Haemodoraceae, Centrolepidaceae, Byblidaceae, Boryaceae, Phylidraceae, Hydatellaceae, which show within Western Australia a clear link between the peinobiomes of the southwest and the sandstone Kimberley region (Figs 7 and 8). Origins of these geographic patterns and their evolutionary significance for the flora assembly of Australia remain still elusive.

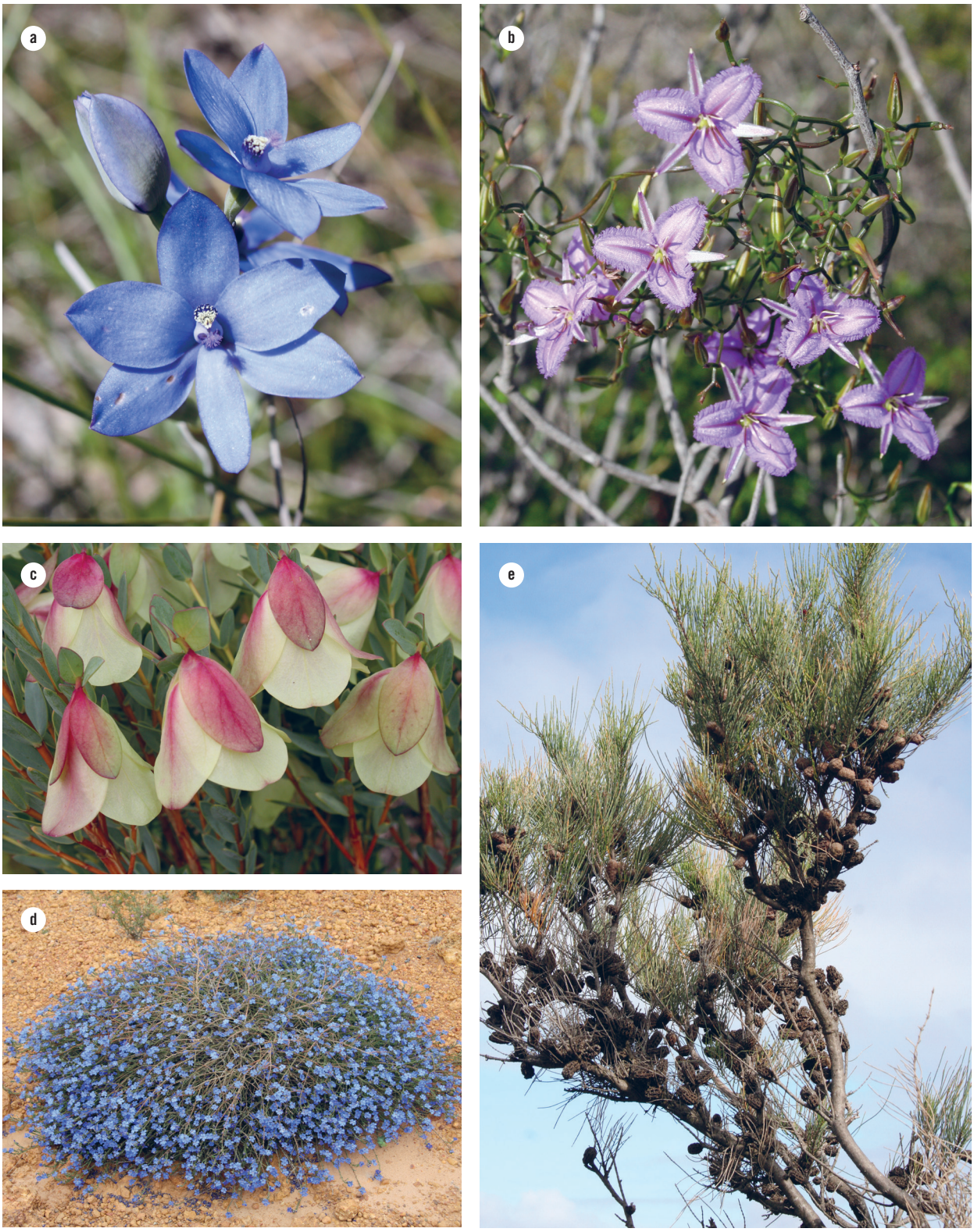


Figure 5A. Representatives of genera typical of the kwongan heath. (a) *Thylemitra cf. crinita* (Orchidaceae), (b) *Thysanotus manglesianus* (Hemerocallidaceae, formerly Laxmanniaceae), (c) *Pimelea physodes* (Thymelaeaceae), (d) *Lechenaultia biloba* (Goodeniaceae), (e) *Allocasuarina fraseri* (Casuarinaceae). Photos: Ladislav Mucina.






Figure 5B. Representatives of genera typical of the kwongan heath. (a) *Anigozanthos manglesii* (Haemodoraceae), (b) *Sphenotoma dracophylloides* (Ericaceae, formerly Epacridaceae), (c) *Macropidia fuliginosa* (Haemodoraceae), (d) *Caladenia arenicola* (Orchidaceae), (e) *Scaevola phlebopetala* (Goodeniaceae). Photos: Ladislav Mucina.

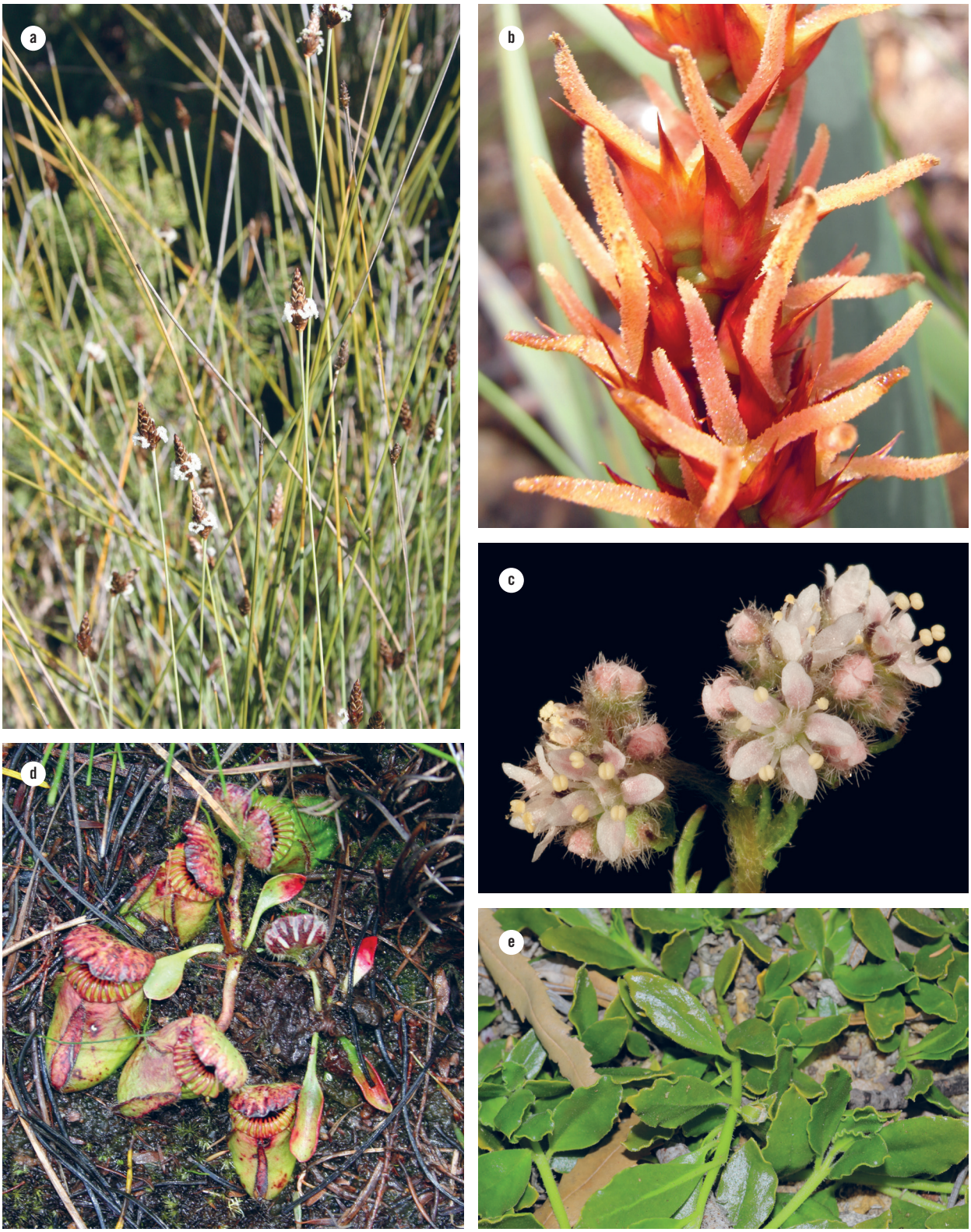


Figure 6A. Representatives of the families (sub)endemic to Southwest Australian Floristic Region (SWAFR). (a) *Ecdeiocolea monostachya* (Ecdeiocoleaceae), (b) *Anarthria scabra* (Anarthriaceae), (c) *Eremosyne pectinata* (Eremosynaceae), (d) *Cephalotus follicularis* (Cephalotaceae), (e) subendemic *Emblingia calceoliflora* (Emblingiaceae), showing odd distribution in SWAFR and then around Exmouth. Photos: a–b, d, Ladislav Mucina; c, Kevin R. Thiele; e, Graham Zemunik.

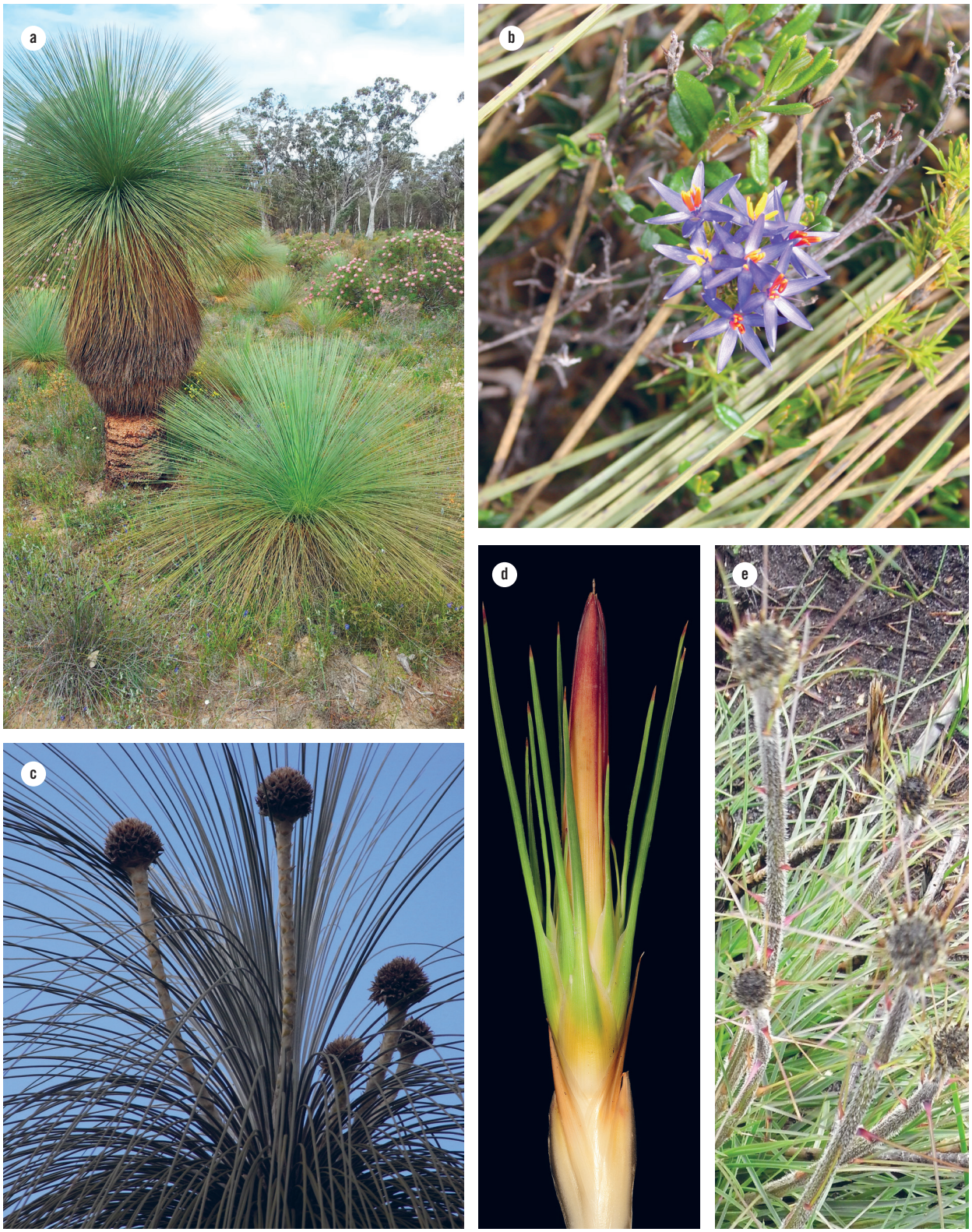


Figure 6B. Representatives of the endemic and subendemic genera of the Dasypogonales occurring in the Southwest Australian Floristic Region. (a) *Xanthorrhoeadrummondii*, (b) *Calectasia narragara*, (c) *Kingia australis*, (c) *Baxteria australis*, (d) *Dasypogon bromeliifolius*. Photos: a, Dagmar Mucina; b-d, Ladislav Mucina.


Figure 7. Representatives of the (sub)endemic Australian families having a centre of diversity in the Southwest Australian Floristic Region and in a secondary centre in the Kimberley peinobiome. (a) *Centrolepis pilosa* (Centrolepidaceae), (b) *Borya sphaerocephala* (Boryaceae), (c) *Conostylis setigera* (Haemodoraceae, Conostyloideae), (d) *Tersonia cyathiflora* (Gyrostemonaceae), (e) *Stylidium elongatum* (Stylidiaceae). Photos: a, Christian Berg, b–e, Ladislav Mucina.

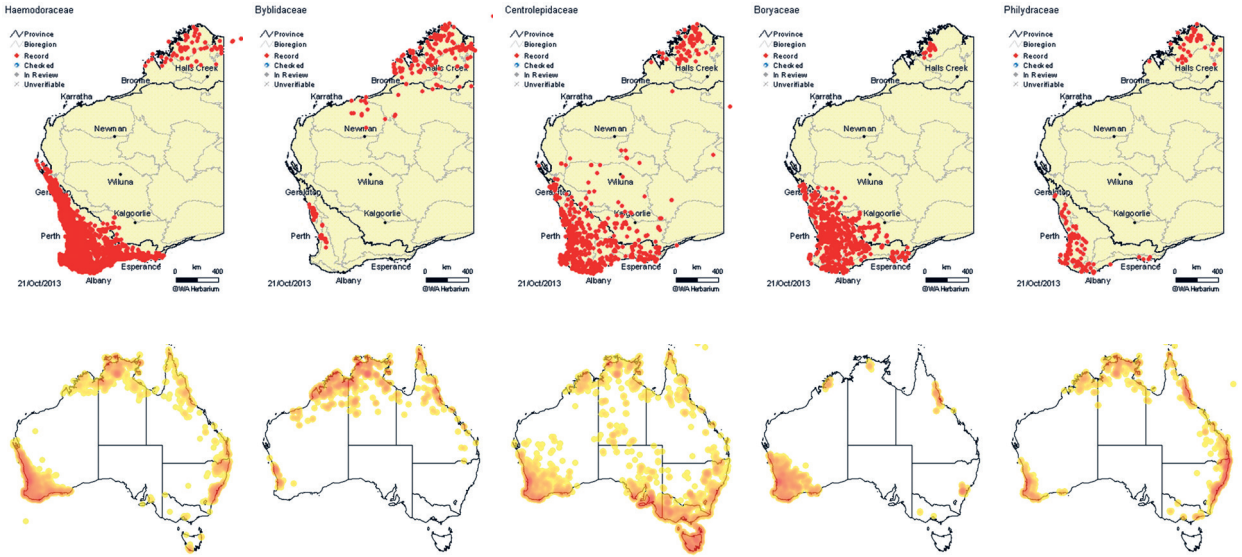


Figure 8. Distribution of selected Australian endemic families in Western Australia (upper row; source: www.dpaw.gov.wa.au/FloraBase) and Australia (lower row; source: Atlas Living Australia; www.ala.org.au), showing the link between the peinobiomes of the warm-temperate Southwest Australian Floristic Region and that of tropical Kimberley region.

While the entire SWAFR has a high level of endemism, analyses of data from specimen records held at the Western Australian Herbarium (Hopper & Gioia, 2004) have identified endemism hotspots within the SWAFR. Plotting the distributions of species with very narrow geographic ranges and controlling for geographic biases in collection effort allowed the identification of four areas – the Mt Lesueur, Greater Perth, Stirling Range and Fitzgerald River areas – where narrow-range endemics are concentrated (Fig. 9). A comparison with the distribution of kwongan in the SWAFR and the inferred patterns of species richness (Fig. 10) suggests that three of these – Mt Lesueur, Stirling Range and Fitzgerald River – are in regions where kwongan is predominant in the landscape and where it occurs in large, contiguous areas. These areas are also close to the coast, have a relatively high current rainfall compared with other kwongan areas, and may have experienced more stable climates than more inland areas: these factors may have allowed the accumulation of narrow-range endemics over time and/or reduced the otherwise high chance of extinction of narrow-range endemics.

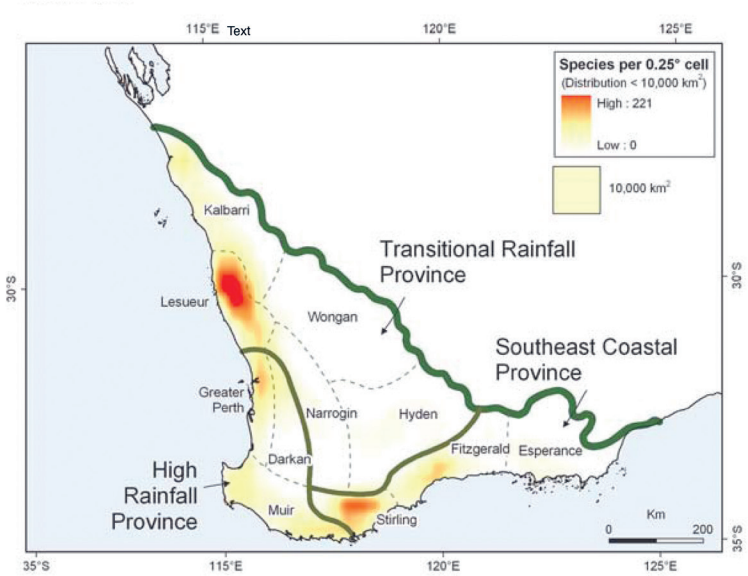


Figure 9. Centres of plant endemism in south-western Australia as approximated by extrapolation of grid data (0.25° latitude x 0.25° longitude) and based on local endemics with geographic distribution occupying < 10.000 km (from Phillips *et al.*, 2011: Fig. 1, based on Hopper & Gioia, 2004).

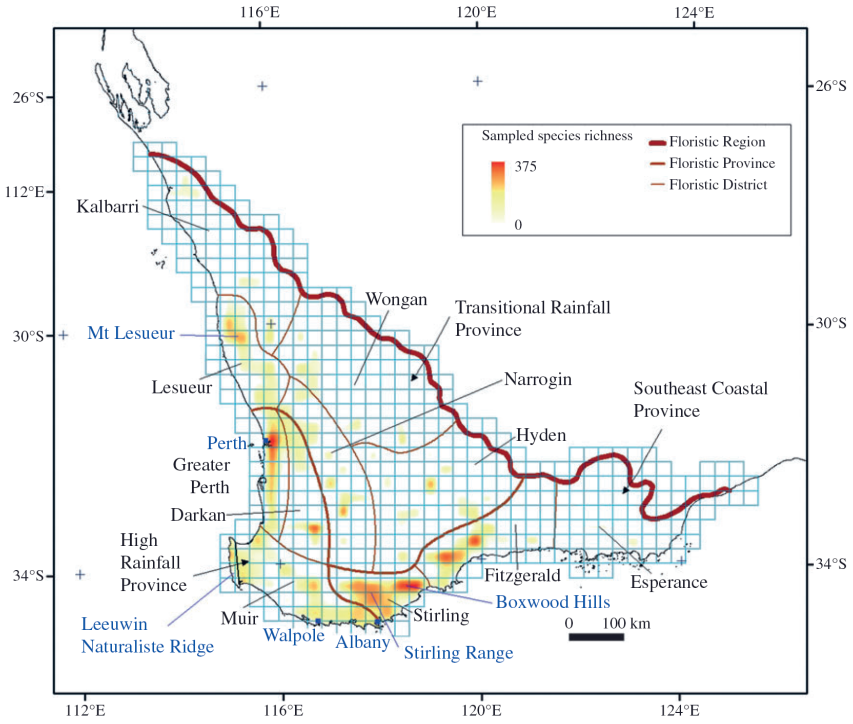


Figure 10. Patterns of species richness towards the background of biogeographic regions of the Southwest Australian Floristic Region. From Phillips *et al.* (2011) as modified after Hopper & Gioia (2004).

## Biogeography of SWAFR and position of kwongan

The areas hosting kwongan in its entirety fall within the Southwest Australian Floristic Region (Takhtajan, 1986). The high rank of the Region has been assigned to SWAFR because of the high scores of endemic families. The fact that the SWAFR is not considered a floral kingdom in its own right (like one would expect because of the African Cape precedent; Good, 1947), but it is merely a region of the Australian Floristic Kingdom, might appear as a paradox, yet the Cape Kingdom status has also been challenged (Cox, 2001; see also Morrone, 2002). The latter author (see also Moreira-Muñoz, 2007) advocated recognition of a broadly-conceived 'Austral kingdom' with another broadly-conceived biogeographic unit called 'Australotemperate region', apparently supposed to accommodate also the current extent of the SWAFR as well as the temperate East Coast and surprisingly also the Wet Tropics of Queensland.

It is an odd tradition to consider biogeographic (spatial) classifications either independent from vegetation-based classifications (usually expressed in form of vegetation maps). A prime example is the obvious discrepancy between Udvardy's (1985: terrestrial biogeographic realms), Takhtajan's (1986: floristic kingdoms and regions) and Meusel *et al.*'s (1965) and Morrone's (2001) influential biogeographic divisions for Europe and South America, respectively, *versus* the biome maps of the world (*e.g.*, Walter & Box, 1976) or vegetation maps of particular continents (Bohn, 2000–2004 and Rivas-Martínez *et al.*, 2004 for Europe; Comer *et al.*, 2003 for North America; Josse *et al.*, 2003 for South America; Sayre *et al.*, 2013 for Africa). Interestingly, the older map of Africa by Frank White (1983, 1993), conceptually resting on biogeographic principles (*e.g.*, centres of endemism, transition mosaics), has been used for a long time in place of an urgently needed vegetation-ecological map. Conversely, and closer to home, the structural vegetation maps (see Beard, 1975 for a summary) served as a basis for definition of the IBRA (Interim Biogeographic Regionalisation of Australia (Thackway & Cresswell, 1995; May & McKenzie, 2003). Beard (1980a) indeed constructed a detailed biogeographic spatial classification scheme encompassing several

levels of complexity. The highest unit called 'provinces' recognised within Western Australia three traditional units (from the East to the West) – Northeast Province, Eremean (Central) Province and Southwest Province. Within the latter, 'floristic districts' (based on vegetation systems) were recognised and named after regional geographic features such as rivers, mountains or botanical celebrities. Beard's biogeographic classification served as a rough basis for the definition of IBRA regions (Commonwealth of Australia, 2005; Ebach, 2012), some to be later divided into subregions.

One sizeable piece of land (about 160,000 km$^2$), including only a small portion of kwongan, has been causing troubles. This region is dominated by eucalypt woodlands, and houses more than 3300 taxa of flowering plants, including 250–350 taxa (depending on source) of *Eucalyptus* and *Corymbia* species. It is warm temperate and characterised by weak a winter-rainfall (approx. 300 mm) regime in the West (IBRA subregion COO2) and transitional winter/summer rainfall in the East (approx. 200 mm) – clearly positioned at a transition between the Mediterranean-type climate of the south-western corner of Western Australia and the semi-desert climate of the Australian interior. The vegetation is often, yet not quite correctly, called 'Mediterranean woodland'. Burbidge (1960) recognised the peculiarity of this region and singled it out as 'South West Interzone'.

## PLANT SPECIES DIVERSITY: PATTERNS AND PROCESSES

One of the most fascinating features of kwongan is the exceptionally high levels of plant species diversity, noted by some of the first botanists who visited the region (Hooker, 1859; Diels, 1906; Gardner, 1944). Plant species diversity is a multi-faceted concept that is best understood with reference to spatial scale (Whittaker, 1975). In particular, kwongan is known for its very high plant species diversity at the local (or community) scale (Lamont *et al.*, 1977), a component referred to as alpha diversity. Moreover, kwongan is also renowned for its very high turnover in species composition between neighbouring communities (Griffin *et al.*, 1983), which is called beta diversity. Together, alpha and beta diversity determine the species diversity across the entire landscape, or gamma diversity (Whittaker, 1960; Tuomisto, 2010) (Fig. 11). In this section, we first describe patterns of alpha and beta diversity in kwongan, comparing them with other species-rich vegetation types in other parts of the world. We present hypotheses about the factors that may be responsible for the maintenance of high alpha and beta diversity in kwongan, while suggesting avenues for future research in that area.

### Alpha diversity

Quantifying alpha diversity can be challenging because a large number of alpha diversity indices exist. Various indices generally differ in their emphasis on species richness (number of species within a community) *versus* evenness (uniformity in the distribution of abundance among species within a community) (Anonymous, 2004). Although some indices that combine richness and evenness are frequently used, there is no consensus as to which measure is best (Magurran, 2004). Moreover, different indices are not comparable to each other. Therefore, we focus here on species richness because it is a fundamental diversity metric that is easy to understand and to compare between studies, is often used in conservation policy and management, and forms the basis of several ecological theories of species

coexistence (Gotelli & Colwell, 2001). Still, despite the apparent simplicity of species richness as an alpha diversity measure, comparing species richness estimates among different habitats must be done with caution. In particular, species richness is highly sensitive to sampling effort (*e.g.*, number of individuals or area sampled) (Gotelli & Colwell, 2001; Magurran, 2004). Therefore, we present information on sampling effort alongside species richness data whenever possible in order to facilitate comparisons.

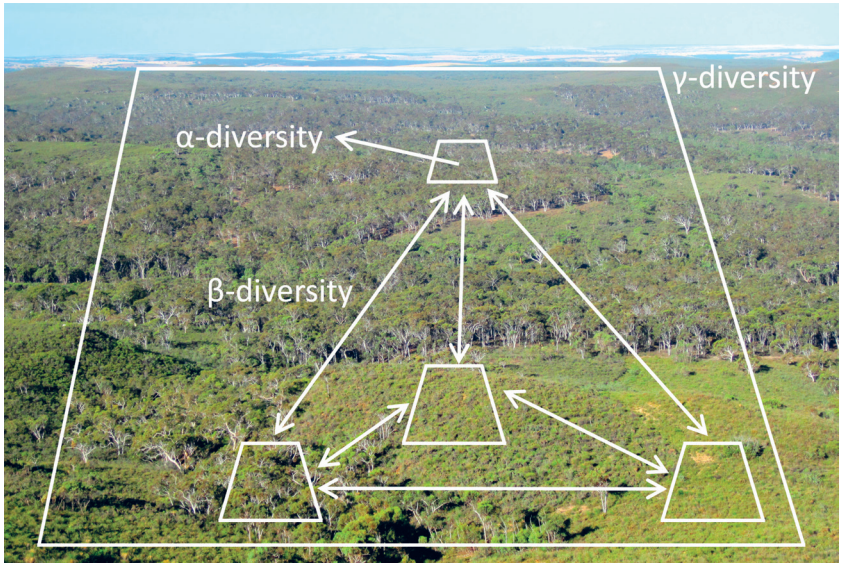


Figure 11. Relationship between alpha (α), beta (β), and gamma (γ) diversity. Alpha diversity is the species diversity (*i.e.* number of species, evenness in distribution of abundance among species) at the scale of a single habitat. This local scale typically corresponds to the scale of an individual plot in a vegetation survey (*e.g.*, ≤ 0.1 ha). Environmental heterogeneity is assumed to be relatively low within a given habitat (*i.e.* the habitat should not encompass environmental gradients) and the habitat should be small enough that individuals could potentially directly interact with each other, for example through resource competition (Huston, 1999). Although some authors have argued for a strict definition of beta diversity (Tuomisto, 2010), beta diversity is broadly defined as the variation in community structure (*i.e.* species composition and abundance) among neighbouring habitats (Whittaker, 1960; Anderson *et al.*, 2011). Finally, gamma diversity represents the total species diversity at the landscape scale which depends on alpha diversity and beta diversity (Tuomisto, 2010). View of kwongan shrublands (in foreground) and wandoo (*Eucalyptus wandoo*) woodlands from the top of Mt Lesueur, near Jurien Bay. Photo: Etienne Laliberté.

## Patterns

The Mt Lesueur & Eneabba, Stirling Range, and Fitzgerald River regions are recognised as the three most species-rich nodes of kwongan vegetation (Hopkins *et al.*, 1983; Hopper & Gioia, 2004). However, kwongan vegetation in the central wheatbelt can be as floristically diverse as these other regions (Brown, 1989). A summary of previous vegetation surveys in kwongan and recorded number of plant species is presented in Table 3. Comparisons among surveys are complicated due to the use of different methodologies (*e.g.*, plot size and shape); however, some superficial comparisons can be made. Based on these surveys, kwongan plant species richness would appear to average ~62 species at 0.01 ha scale (Table 3). At a broader 0.1 ha scale, kwongan contains ~86 species. However, these figures must be interpreted with caution as they come from a limited number of surveys.

Table 3. Summary of vegetation surveys in kwongan and number of plant species recorded. In all studies only vascular plants were counted. The high species richness* in Lamont *et al.* (1977) reflects the use of long transects used that maximise environmental variation.

| STUDY | SOIL TYPE/HABITAT | REGION | PLOT SIZE | NUMBER OF PLOTS | NUMBER OF SPECIES |
|---|---|---|---|---|---|
| Lamont *et al.* (1977) | Sand over yellow-brown clay | Eneabba | 0.05 ha (500 1–$m^2$ quadrats along a 1500–m transect) | 500 1–$m^2$ quadrats along a 1500–m transect | 172* |
| Hnatiuk & Hopkins (1981) | Clay, deep sand or lateritic gravel | Mt Lesueur and Eneabba | 0.1 ha | 87 | 15–129 |
| Brown & Hopkins (1983) | Grey and yellow sand, laterite and duplex soils | Tutanning Nature Reserve | 0.01 ha | 13 | 32–70 (average = 54) |
| Brown & Hopkins (1983) | Grey and yellow sand, laterite and duplex soils | Tutanning Nature Reserve | 0.05 ha | 12 | 49–91 (average = 73) |
| Brown & Hopkins (1983) | Grey and yellow sand, laterite and duplex soils | Tutanning Nature Reserve | 0.1 ha | 12 | 59-103 (average = 83) |
| Griffin *et al.* (1983) | Laterite | Mt Lesueur and Eneabba | 0.01 ha | 31 | 33–87 (average = 70) |
| Griffin & Hopkins (1985) | Laterite | Top of Mt Lesueur | 0.01 ha | 5 | 109 (combined for the five plots) |
| Brown (1989) | Laterite | Central Wheatbelt (40,000 $km^2$) | 0.1 ha | 20 | 64–124 (average = 91) |
| Perry *et al.* (2008) | Dune crest, dune swale, laterite, limestone | Eneabba | 0.16 ha (limestone and crest) 0.09 ha (laterite and swale) | 4 | 74 (limestone) 113 (crest) 93 (laterite) 104 (swale) |

How does the alpha diversity of kwongan compare to that of other Mediterranean ecosystems? Fynbos in the Cape Flora of South Africa, also a species-rich vegetation type, is perhaps the most similar Mediterranean ecosystem to kwongan outside Australia (Bond, 1983). Taylor (1972, p. 197) recorded 121 plant species in 0.1 $ha^{-1}$ in fynbos (see Box 1) shrublands, and this figure has often been quoted to support the high alpha diversity of fynbos (Bond, 1983, p. 198). Based on previously published surveys (Table 3), such high alpha diversity would appear to be much greater than what is found in kwongan. However, Bond (1983, p. 198) suggests an average of 63 plant species / 0.1 ha in fynbos which is similar, if not lower than that found in kwongan (Table 3). Despite the uncertainty associated with these figures, due to small sample sizes, it is well established that both kwongan and fynbos show higher alpha diversity than other Mediterranean vegetation types (Bond, 1983; Cowling *et al.*, 1996), perhaps with the exception of some grazed shrublands in Israel (Naveh & Whittaker, 1980). In addition, Lamont *et al.* (1977) showed that several alpha diversity indices calculated for kwongan were higher than those for other species-rich vegetation types in the world.

## Processes

What can explain the high alpha diversity in kwongan? Determining which factors are responsible for the coexistence of plant species in local communities is a topic of high interest in ecology (Laliberté *et al.*,

2013), as highlighted by >100 hypotheses that have been proposed (Palmer, 1994). Here, we highlight some of the main hypotheses that may apply to kwongan in particular. To a large extent, these hypotheses were previously proposed by Lamont *et al.* (1984), with some new additions.

**Large species pool:** The number of species that actually coexist in a local habitat is, obviously, constrained by the number of species that can potentially colonise the site – otherwise known as a 'species pool'. Some ecologists have proposed that the size of species pools is the primary determinant of alpha diversity (*e.g.*, Zobel *et al.*, 2011). As such, the high alpha diversity of kwongan could be partially explained by its large species pool. That said, while a community clearly cannot show high alpha diversity if its species pool is very small, a large species pool does not necessarily imply high alpha diversity, because local factors that prevent dominance and competitive exclusion also need to operate (Huston, 1999). Such factors are described next.

**Low productivity:** Most of kwongan is found on soils that rank among the least fertile in the world. Of all plant nutrients, phosphorus (P) in particular is especially limiting in soils which are very old and strongly weathered (Lambers *et al.*, 2010; Laliberté *et al.*, 2012). In addition, low rainfall, high potential evapotranspiration and sandy soils with low water-holding capacity mean that water deficits are a common feature in kwongan (chapter 5). Consequently, plant productivity in kwongan is generally low, restricting opportunities for dominance by any one species and thus promoting species coexistence. Such a 'productivity-diversity' explanation is in line with classical theories of plant species coexistence (Grime, 1973; Huston, 1979).

**Disturbances:** Selective disturbances, such as grazing, can promote species coexistence, if they affect dominant species more than rare species. However, even non-selective disturbances such as fire can promote species coexistence by slowing down competitive exclusion (Huston, 1994). Fire occurs frequently in kwongan (chapter 6), and therefore may contribute to high alpha diversity in that manner. In addition, fire in kwongan may also promote local plant species coexistence by creating 'regeneration niches' (Enright *et al.*, 2007). On the other hand, excessive fire frequency can lead to local extinctions and thus reduce alpha diversity.

**Resource partitioning and facilitation:** Phosphorus is the key limiting nutrient in kwongan (chapter 4). Although plants take up P as inorganic phosphate, P occurs in soil in many inorganic and organic forms (Turner, 2008). Kwongan plant species show a high degree of functional diversity in P-acquisition strategies, and species with different strategies might preferentially target particular P pools (Lambers *et al.*, 2010). Therefore, partitioning for soil P might reduce inter-specific competition relative to intra-specific competition, thus promoting plant species coexistence in low-P soils (Turner, 2008). In addition, it is possible that non-mycorrhizal Proteaceae, which are particularly abundant in kwongan, might facilitate neighbouring plants by mobilising scarcely available micronutrients (Muler *et al.*, 2014). Resource partitioning for P, and facilitation of nutrient uptake by Proteaceae, deserve further attention in kwongan.

**A role for soil-borne pathogens?** There is evidence from species-rich plant communities such as tropical rainforests that seedlings of one species perform poorly near conspecific individuals, relative to individuals from other species (Comita *et al.*, 2010). Such negative density dependence can promote species coexistence because it keeps dominant species 'in check'. It is being increasingly recognised that species-specific soil-borne pathogens can be responsible for such negative density dependence (Mangan *et al.*, 2010; Kardol *et al.*, 2013). Although introduced pathogens such as *Phytophthora cinnamomi* can have strong negative impacts on plant diversity in kwongan (chapter 8), it might be that less virulent native soil-borne pathogens alter the

competitive balance among neighbouring plants in a way that promotes species coexistence. Whether such a mechanism occurs in kwongan is unknown, but warrants further investigation.

## BETA DIVERSITY

Kwongan is renowned for its very high beta diversity. A number of vegetation studies from the 1980s in the Mt Lesueur & Eneabba region have highlighted the high spatial variability in plant community composition (*i.e.* beta diversity) among neighbouring stands in kwongan (Hnatiuk & Hopkins, 1981; Griffin *et al.*, 1983; Hopkins & Griffin, 1984). For example, plant communities just a few hundred meters apart may share fewer than 40% of their species (Griffin *et al.*, 1983). In fact, it was found in that study that pairs of sampled sites rarely shared more than 45% of their species (Griffin *et al.*, 1983). Such high beta diversity is remarkable, given the subdued topography of the landscape and the apparent uniformity of the sandy soils, which are all invariably low in nutrients (Hopkins & Griffin, 1984). What drives this high beta diversity in kwongan?

Environmental control is the most common explanation for spatial patterns in plant community composition across the landscape. However, such 'environmental determinism' was questioned by Hubbell's (2001) neutral theory, which proposed that random but spatially limited dispersal generates beta diversity. While it is unquestionable that environmental controls (*e.g.*, climate, soils) drive changes in community composition at broad spatial scales, the key question here is whether such controls are also important at smaller spatial scales of a meta-community, where neighbouring communities are linked to each other by dispersal (Holyoak & Loreau, 2006; Laliberté *et al.*, 2009).

The available data does not suggest strong edaphic control of beta diversity in areas of kwongan, at least not at spatial scales considered in surveys. For example, Hnatiuk & Hopkins (1981) found that only 6% of the variation in community composition in kwongan sites south of Eneabba could be explained by variation in soil type. Similarly, in a study of kwongan from the eastern Roe Botanical District, Burgman (1988) found little association between variation in soil physical and chemical properties (*e.g.*, pH, total soil N, P and K) and plant community composition. Using a modelling approach parameterised from high-resolution vegetation survey data, Perry *et al.* (2009) concluded that local dispersal limitation (coupled with broader-scale edaphic fidelity) best explains spatial variation in community composition within kwongan. Together, these results suggest that beta diversity within an area of kwongan primarily reflect the vagaries of dispersal and historical legacies (*e.g.*, effect of previous disturbances such as fire). Soil physical properties (*e.g.*, water-holding capacity, soil depth), however, probably play an important role in driving species distributions in kwongan (Hopkins & Griffin, 1984; Groom, 2004).

Few significant advances in determining the drivers of beta diversity in kwongan have been made since Hopkins and Griffin (1984). Clearly, more work is required to determine the relative importance of different processes. It might be that plant species distributions respond to soil properties that have not been well characterised in previous surveys, including a potential role of soil biota (Klironomos *et al.*, 2011). Still, an important lesson from the studies conducted so far is that the design of nature reserves in kwongan on the basis of soil maps alone is not sufficient to ensure that a range of plant species and community types will be preserved (Burgman, 1988).

## COMPLEXITY OF VEGETATION PATTERNS

The complexity of kwongan has many dimensions: distributional, ecological, floristic and structural. Biogeographically, the core of the deep sand and laterite kwongan occurs in the Irwin and Eyre Botanical Districts. The largest portions of kwongan shrublands are found within the Irwin region housing Northern Sandplains and the Eyre region – home to Southern Sandplains (Fig. 12).

In the Irwin it also occurs in inland regions of Avon, Roe and Coolgardie District, here found in complex with wheatbelt woodlands, mallee shrublands and Great Western (Goldfields) Woodlands, respectively. Interestingly, it appears that kwongan (dominated by *Verticordia* and *Banksia*) does occur on deep red sand on ridges of inland sand dune systems as far north as Exmouth and northeast of Carnarvon (Fig. 13a).

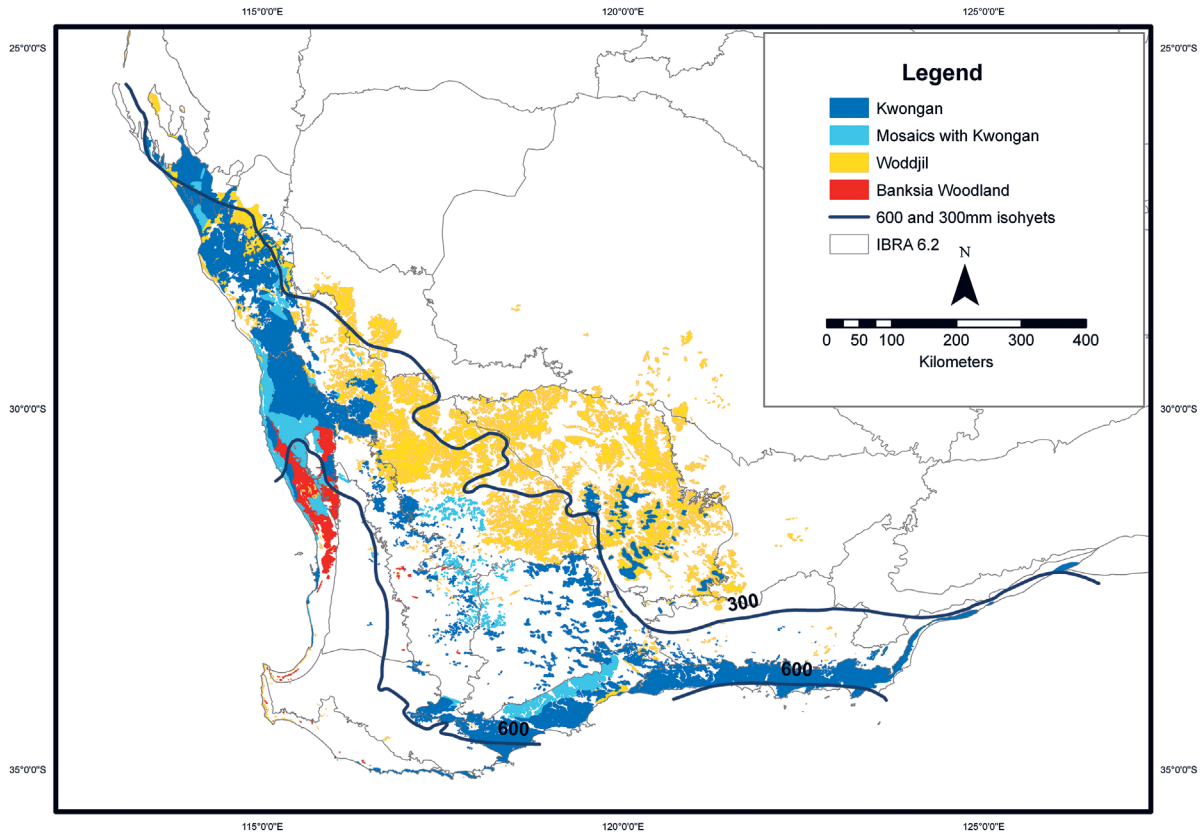


Figure 12. Distribution of kwongan vegetation types and mosaics of kwongan and other vegetation types. Spatial data based on published and unpublished mapping by J.S. Beard (Shepherd, 2003; Beard *et al.*, 2013). The 'mosaics with kwongan' relate to small-scale spatial mosaic of kwongan heath and *Banksia* woodlands (and possibly also wodjil) on the Northern Sandplains and the mosaic between kwongan heath and mallee scrub on the Southern Sandplains. Wodjil appears as dominating shrubland in the northern wheatbelt and the western part of the Great Western Woodlands.

## BEARD'S CLASSICAL STRUCTURAL-PHYSIOGNOMIC APPROACH

### Basics

Understanding the complexity of vegetation of Western Australia would be unthinkable without appreciating the contribution of J.S. Beard. Beard has won his international reputation by championing the vegetation-structural approach to vegetation classification (Beard, 1973a) and for its convincing application of this approach to vegetation mapping (see Beard, 1975a for a milestone summary). The elements of vegetation structure involve dominating growth-forms, and density of vegetation canopy. Why did Beard give preference to structure and not floristics? Because it is obviously not difficult to distinguish trees from shrubs, grassy understorey from tree layer, and dense from sparse canopy cover having a couple of conventional rules at hand. It is less common that vegetation surveyors have sufficient command of plant taxonomy or experience involving knowledge of flora and/or possess ecological data of quality allowing putting floristic composition of plant communities into context of local and regional ecological gradients and potential drivers of the vegetation patterns. Using the structural approach is then quicker, at least in the field-sampling phase. Yet it is not devoid of problems and inconsistencies.

Kwongan is a structurally complex, in a way 'multilayered' vegetation type (Beard 1981, p. 78–79). Although some structural types of kwongan do have clearly distinguishable vertical layers (*e.g.*, mallee-heath or *Banksia* woodland), the vertical layering is obscure for most parts – a feature shared with analogous sclerophyllous scrub such as garrigue in the Mediterranean basin or South African fynbos. In Beard's terminology (Beard, 1981), kwongan can occur in any of the Canopy Density level of S or Z (S: Shrubs, Z: Heath) Life Form/Height Class categories in communities with a significant single layer. For those with more than one significant layer, kwongan covers all categories called 'Heath' – with trees, shrubs, and mallee, respectively.

Beard has translated his vegetation-structural/physiognomic classification approach into several series of vegetation maps, which feature the kwongan shrublands in particular on the 1:1,000,000 Sheet 7 Swan (Beard, 1981) as well as on Sheets 4 Nullarbor (Beard, 1975b) and Sheet 6 Murchison (Beard, 1976b). The 1:250,000 series (Beard, 1972a–e; 1973b, c; 1976c–g; 1979a–d; 1980b–e) shows in detail the distribution of various kwongan shrublands (including wodjil thickets and *Banksia* woodlands) in the southwest of Western Australia.

Beard's vegetation maps are considered to follow a vegetation-structural approach, yet this cliché is misleading. Indeed formations are basic classification vegetation units (and here lies the largest problem with Beard's classification); however, by subdividing the structural formations into 'associations' reflects Beard's understanding of importance of local floristic composition to recognise local vegetation types – implicitly recognising the hierarchical nature of ecological driving forces. Using the formations along regional (landscape-level) environmental catenas yielded a useful spatial term – vegetation system (Box 1). Ordering of formations into vegetation systems reflects Beard's understanding of importance of geographic dimension of vegetation variability, while ordering of formations into vegetation series reflects Beard's understanding of the importance of soil patterns and their interaction with climate in driving the vegetation patterns.

### Beard's legacy today

Beard (1990) himself summarised his vast knowledge of the vegetation of the State in a well-illustrated book *Plant life of Western Australia*. His mapping and classification work has been summarised (and

partly revised) by Hopkins *et al.* (2005) who created a database storing information at a scale of 1:250,000 recognising 2950 basic map units or 'system-associations' with 2173 associated unique vegetation descriptions. At the next level in this system is the author's grouped 818 Vegetation Associations, further agglomerated into Alliances, supposed to be appropriate for use at the 1:1,000,000 scale. The Alliances further agglomerate into 50 Formations, which form the basic map units appearing on the new 1:3,000,000 scale vegetation map of Western Australia, with accompanying memoir posthumously published by Beard *et al.* (2013).

Physiognomy/structure is still dominating classification paradigm at the Commonwealth level and therefore the National Vegetation Information System (NVIS) system (ESCAVI 2003; http://www.deh.gov.au/erin/nvis) and there is no doubt that the adoption of the six-tier system where classification Levels I through IV are dominated by vegetation-structural/physiognomic criteria root in the work of J.S. Beard and R. Specht (1970; 1983). The implementation of the ESCAVI system found its implementation also in Western Australia (Shepherd *et al.*, 2002; Shepherd, 2003).

## FLORISTIC CLASSIFICATION OF VEGETATION PATTERNS: BEYOND BEARD

Beard's lifetime achievements are undisputable; yet, the tides are changing and the new challenges posed by new threats (biodiversity demise, climate change) are calling for application of new, more precise and sophisticated methodologies. Despite all the merits and the monumental extent of the work, Beard's vegetation classification, built on the system of formations, associations, as well as vegetation systems and vegetation series (for definitions see Box 1), fails to reflect the relative importance of the current ecological fabric and especially to incorporate successfully the biogeographic (evolutionary-assembly) aspects of vegetation complexity. It sounds logical that the classification (and mapping) of vegetation should use primarily the information content of the ecologically and evolutionarily most informative constituents such as species (or taxa). It is, however, also understandable that in those parts of the world where the floras are insufficiently known, criteria other than floristic ones would be preferred (Ross Cochrane, 1963; Beard, 1973a; Specht 1970, 1983; George *et al.*, 1979; Beadle, 1981; Carnahan, 1990).

The floristic-sociological approach to vegetation classification in Western Australia has not set such deep roots as in the Northern Hemisphere (*e.g.*, Westhoff & Van der Maarel, 1973; Van der Maarel, 1975; Mucina, 1997) or in South Africa (*e.g.*, Werger, 1976; Mucina & Rutherford, 2006). Beard was not known for amassing large collections of plot-based vegetation data. In fact his manuals to the regional (1:250,000) vegetation maps do not contain any vegetation plot-based sample (or relevé). Yet, Beard did make use of his vast floristic knowledge to distinguish (and informally describe) floristic vegetation patterns at low levels of the vegetation-classification hierarchy.

The importance of inventories aimed at surveying and describing vegetation patterns was also recognised by resident Western Australian vegetation scientists (*e.g.*, Hnatiuk & Hopkins, 1981; Brown & Hopkins, 1983; Griffin *et al.*, 1983; Brown, 1989). All these studies address kwongan vegetation and use a more formal approach to vegetation survey, including adoption of plot-based sampling design, formal (numerical) data analysis, and community entitation (= recognition) of the vegetation units (*sensu* Peet & Roberts, 2013). Yet, many of those surveys fall short of proceeding to the level of cluster assessment,

community characterisation and determination (including formal naming and assignment to a vegetation classification system).

Vegetation surveys incorporating plot sampling aimed at gathering data on co-occurrence of species in relation to habitat properties have gained momentum especially through the Biodiversity Programme aimed at surveying either nature reserves (see many unpublished and published reports made available through the NatureMap) or of biodiversity importance yet poorly covered by data or special habitat complexes under imminent threat such as Banded Iron Formations (Keighery *et al.*, 2007). Many of the reports (and published papers, especially on pages of the Conservation Science Western Australia; available open access through http://dpaw.wa.gov.au) contain valuable data that, one day, would serve a State-wide vegetation survey and aid building of a unified vegetation classification system for Western Australia.

Foundations for the floristic-sociological syntaxonomic system (see Westhoff & Van der Maarel, 1973; Weber *et al.*, 2000 for terminology and concepts) of the kwongan vegetation, were laid by European phytosociologists in the 1980s (Bridgewater & Zammit, 1979; Bridgewater & Backshall, 1981; Pignatti *et al.*, 1993). A skeleton of such a system featuring the vegetation diversity of Western Australia has been summarised by Pignatti & Pignatti (1990; 1996; 1997). Kwongan vegetation appears in this system summarised as the *Banksio–Dryandretea niveae* (including sandplain and laterite kwongan and *Banksia* woodlands) and the *Spyridio–Melaleucetea acerosae* (including lime-rich dune and calcrete kwongan).

## KWONGAN IN ZONALITY/AZONALITY FRAMEWORK

The term *biome* has been used in connection with SWAFR and its vegetation types for a long time, usually by identifying SWAFR with the 'Mediterranean biome' (part of the global Big Five of the Mediterranean-type ecosystems; *e.g.*, Cowling *et al.*, 1996) and sometimes including also the Interzone as a part of 'southwest Australian Mediterranean biome' (Judd *et al.*, 2008). We suggest that these are grossly simplistic views that do not follow the current use of the term in which macroclimate (and the filtering effect of it selecting for combination of life forms) plays the central role. The argument that SWAFR (with kwongan as one of the flagship vegetation types) is 'Mediterranean' simply because it has winter-rainfall seasonality might be misleading since the winter-rainfall does not define the 'Mediterranean-type biome' (Blumler, 2005).

Applying the zonality/azonality (including intrazonality and extrazonality) conceptual framework of Walter (Walter, 1964; 1973; 1979; Walter & Box, 1976; Walter & Breckle, 1991), and considering the modern definition of biome (*zonobiome* in Walter's terminology) 'viewed as a high-level hierarchical unit having a similar vegetation structure exposed to similar macroclimatic patterns, often linked to characteristic levels of disturbance such as grazing and fire' (Rutherford *et al.*, 2006), we redefine the biome structure of the SWAFR and pin-point the position of kwongan shrublands in this system.

The climate (seeing as a complex of environmental filters) influences the formation of the plant cover and that of the soils. Thus, the zonobiomes are characterised not only by the climate, but also by the zonal vegetation and the zonal soil types. Pedologists point out, however, that within soil-type zones, large areas with intrazonal and azonal soils often appear, the formation of which is determined less by the climate than by the material of the substrate (*e.g.*, sand, shallow rocky soil, peat) or by other local factors (*e.g.*, high groundwater level, salt concentration of groundwater). On such soils one also finds azonal

vegetation, deviating from zonal vegetation. Walter (1973) recognised that there are extensive regions around the world where soils modify the zonal vegetation patterns. For the regions where extremely nutrient-poor soils determine the physiognomy, structure, indeed functioning of the vegetation, Walter suggested to use the term 'peinobiome'. SWAFR should be considered as one of the most prominent examples of a peinobiome.

In the new scheme of major vegetation types in SWAFR and their classification into the zonal-biome framework, we recognise three zonal biomes (Table 4):

- Austral Sclerophyllous Warm-Temperate Forests
- Austral Sclerophyllous Warm-Temperate Woodlands
- Kwongan Sclerophyllous Scrub

Some (but not all) of the major communities recognised within these biomes are members of the south-western Australian Peinobiome (Table 4) – kwongan shrublands are among the most prominent of all.

## A SIMPLIFIED PHYSIOGNOMIC CLASSIFICATION OF KWONGAN SHRUBLANDS

Here we offer an alternative for the informal classification of the kwongan vegetation, relying rather on the dominant shrub and/or graminoid life form element instead of focusing on vertical vegetation layering. We concur with Beard's definition of kwongan (in a broad sense) and consider, besides the kwongan heath (scrub, mallee-heath, thicket) proper also *Banksia* woodlands and wodjil thickets.

### Kwongan heath

Beard (1981: 117) suggested that there is no simple climatic zonation of vegetation in south-western Australia, the climatic position of most of the kwongan heath (kwongan *sensu stricto*) (Table 4) are concentrated in a region spanning 450 mm and 625 mm of mean annual precipitation – in a Transitional Rainfall Zone as defined by Hopper (1979; see also Fig. 12). Less obvious becomes the climatic niche of kwongan when also wodjil shrublands are incorporated; the latter vegetation type is spatially the most prominent mapping unit on the Swan vegetation mapping sheet (Beard, 1981, p. 144).

The ecological position of kwongan along regional soil catenas was elucidated by Beard (1981, pp. 115–129) by his vegetation-series approach. If kwongan is determined by the occurrence of sandy, gravelly and ferruginous substrates at rainfall of 450–625 mm, then there is a sudden 'cut-off' point detectable along four of five vegetation series as defined by Beard (1981, pp. 126–129). The sudden nature of this cut-off point is presumed to be driven by moisture-retaining capacity, rather than by soil nutrients as most of the plant communities forming the vegetation series on substrates in south-western Australia are supported by nutrient-poor soils, and hence kwongan is only one of the elements of the south-western Australian peinobiome (Walter & Box, 1976).

Following a simple principle of the dominating family (or morphologically similar families such as graminoid Cyperaceae, Restionaceae and Anarthriaceae), we may distinguish: myrtaceous-proteaceous kwongan, grasstree kwongan, and sedge kwongan (Figs 13a, b). How informative this vernacular classification might be ecologically shall be tested by a new, badly needed, floristic classification of kwongan, based on real plot data.

Depending on substrate and water regime we can distinguish a number of kwongan types, such as Bassendean Sandy, Calcrete, Coastal Dune, Laterite, Granite Heath (*e.g.*, Keighery *et al.*, 2002), Stirling Sandstone, Tumblagooda Sandstone and Swamp kwongan types (Figs 14a, b). The quality of substrate (geology) reflects in specific soil conditions that translate into different floristic patterns. The tradition so far was to distinguished sand kwongan shrublands, those on laterites, and perhaps a transitional type. Most of the kwongan types distinguish on substrate are purely terrestrial; however, kwongan occurs (in form of sedge kwongan and/or myrtaceous-proteaceous kwongan) also in temporary wetlands, with the best examples perhaps found embedded with the precipitation- and forest-rich Warren region.

## Banksia woodlands

*Banksia* woodlands (Fig. 14) are geographically, physiognomically, and partly also ecologically slightly different from other types of kwongan shrublands. Geographically, they are limited to coastal regions north and south of Perth, mainly to the Swan Coastal Plain and reach as far north as the Dandaragan Plateau (Fig. 12). They invariably occur on deep, mainly Bassendean but also Spearwood sands (Semeniuk & Glassford, 1989). The floristic and life form composition of the undergrowth basically matches open kwongan heath. Because they occur in regions with shorter dry season (5–6 months; Beard, 1989) and receive higher precipitations than the core regions of the kwongan heath (Northern and Southern Sandplains), the overstorey is formed by low (5–8 m tall) trees among which *Banksia attenuata*, *Banksia menziesii* (especially in the South) and *Banksia hookeriana* and *Xylomelum angustifolium* (in the North), accompanied regularly by *Nuytsia floribunda* (see Havel, 1968; Gibson *et al.*, 1994; Dodd & Griffin, 1989). Close floristic relationship between the kwongan heath and the *Banksia* woodlands is also expressed in the syntaxonomic system by Pignatti & Pignatti (1996, 1997) who classified both vegetation types within the same phytosociological class – the *Banksio-Dryandretea niveae*.

The *Banksia* woodlands are presumed to have occupied almost 7000 km$^2$, of which only about 30–40% has been present until today (Beard & Sprenger, 1984).

## Wodjil thickets

Wodjil (Fig. 14a) is a vegetation type that has, so far, not received as much attention as the kwongan heath. Yet, it is (or has been) potentially, according to Beard (1981, mapping sheet 7) the most extensive type of the kwongan shrublands (*sensu lato*). The lack of scientific interest could be ascribed to lower species richness (when compared to kwongan heath) as well as of the small current extent of the remnants. Wodjil has been in the past a prime target of scrub clearing (see Beard, 1981) and the best patches survive either in nature reserves on and around granite outcrops or in broad road reserves within the wheatbelt and in the western part of the Great Western Woodlands.

The appearance of these shrublands is often 'broomy' (characterised by deep position of the shrub ramification, creating a broom-like or broad umbrella-like canopy), which brought them the name 'broombush thickets', 'tammar-wodjil thickets', '*Acacia–Casuarina* thickets', '*Acacia resinomarginea* thickets', '*Casuarina-Calothamnus* thickets', '*Causarina campestris* thickets' (Western Australia; *e.g.*, Beard, 1981, pp. 128–129), or 'broombush shrubland' in South Australia (Berinkshaw, 2009, pp. 102–103). The structural term 'thicket' goes well with wodjil since these shrublands are indeed very thick (show highly closed canopy).

Wodjil is not equivalent to mallee shrublands, which are also a tall-grown scrub, yet dominated by

| BIOME | MAJOR VEGETATION TYPES | NATURE OF ZONALITY | FIRE REGIME |
|---|---|---|---|
| Austral Sclerophyllous Warm-Temperate Forest | Karri & Tingle Forest | zonal | understorey fire |
| | Jarrah & Marri Forest | zonal; part of SW Australian Peinobiome | understorey fire |
| Kwongan Sclerophyllous Scrub | Kwongan Shrubland | zonal; part of SW Australian Peinobiome | canopy fire |
| | Banksia Woodland | zonal; part of SW Australian Peinobiome | understorey & canopy fire |
| | Woodjil Thicket | zonal; part of SW Australian Peinobiome | canopy fire |
| | Swamp Heath | intrazonal (driving influence of seasonal waterlogging and flooding); part of SW Australian Peinobiome | canopy fire |
| Austral Sclerophyllous Warm-Temperate Woodland | Goldfieldd Eucalyptus Woodland | zonal | understorey fire |
| | Wandoo Sclerophyllous Woodland | zonal; part of SW Australian Peinobiome | understorey fire |
| | Mallee Scrub | zonal | canopy fire |

Table 4. New system of major vegetation types grouped into zonal biomes for the SWAFR. C: canopy, U: understorey.

| | GROWTH-FORMS | VEGETATION STRUCTURE | SOIL (GEOLOGY) & HYDROLOGY |
|---|---|---|---|
| | C: very tall trees with sclerophyllous leaves | C: closed canopy; up to 80 m | deep yelow clays on granite |
| | U (shrub): malacophylous tall shrubs | U (shrub): dense thicket | |
| | U (herb): creeping herbs | U (herb): very sparse | |
| | C: medium-tall trees with sclerophyllous leaves | C: closed canopy | shallow red soils on laterite |
| | U1 (shrub): sclerophyllous shrubs | U1 (shrub): sparse | |
| | U2 (herb): ephemeral herbs, prostrate dwarf shrubs | U2 (herb): very sparse | |
| | C: low shrubs and occasionally admixed tall shrubs; dwarf shrubs in coastal wind-pruned scrub | C: closed canopy, between 0.1 (coastal windpruned kwongan) to 2 m (scrub-heath) | leached sandy soils over laterite, sandstone, granite and metamorphic rocks; often on rocky outcrops as well |
| | U1: low (creeping of prostrate) shrubs; bulbous herbs, ephemeral herbs, dwarf | U2: very sparse | |
| | C: low trees with sclerophylous leaves | C: closed canopy, between 0.1 (coastal windpruned kwongan) to 2 m (scrub-heath) tall | deep Bassendean soils; ridges of dunes; shallow calcarous sands over porous calcrete and aeolinite |
| | U1: sclerophyllous shrubs | U2: sparse to dense | |
| | U2: low (creeping of prostrate) shrubs; bulbous herbs, ephemeral and perennial herbs | U2: very sparse | |
| | C: tall shrubs with sclerophyllous leaves | C: closed canopy, 2–4 m tall | coarse grained sandy soils mainly derived from granite; also on greenstones and BIFs |
| | U: ephemeral herbs | U: very sparse | |
| | C: sedges | C: closed canopy, up to 1 m tall | clayed layer over deep sand or laterite; seasonally wet or flooded |
| | U: creeping herbs | U: sparse | |
| | C: low and medium-tall trees with sclerophyllous leaves; both resprouters and reseeders | C: semi-open canopy; up to 18 m | prevalently deep sandy soils with varying level of clay (depending on landscape position) and varying degree of salinity |
| | U (shrub): sclerophyllous or semi-succulent (chenopods) shrubs | U (shrub): sparse to very dense (chenopod) | |
| | U (herb): annual and bulbous hersb; rarely prostrate and creeping shrubs | U (herb): mostly very sparse (mainly due to high cover of litter); in places rich spring annual herb synusia | |
| | C: low and medium-tall trees with sclerophyllous leaves | C: semi-open canopy; up to 20 m | shallow red soils on laterite |
| | U1 (shrub): medium-tall to tall sclerophyllous shrubs | U1 (shrub): sparse to dense | |
| | U2 (herb): ephemeral herbs, prostrate dwarf shrubs | U2 (herb): very sparse | |
| | C: tall clonal, multistemmed resprouting eucalyptus shrubs of mallee form | C: closed canopy; up to 3–5 (8) m tall | duplex soils (sand over acidic clay layer) |
| | U: annual herbs | U: very sparse; occassionally spring herb synusia | |

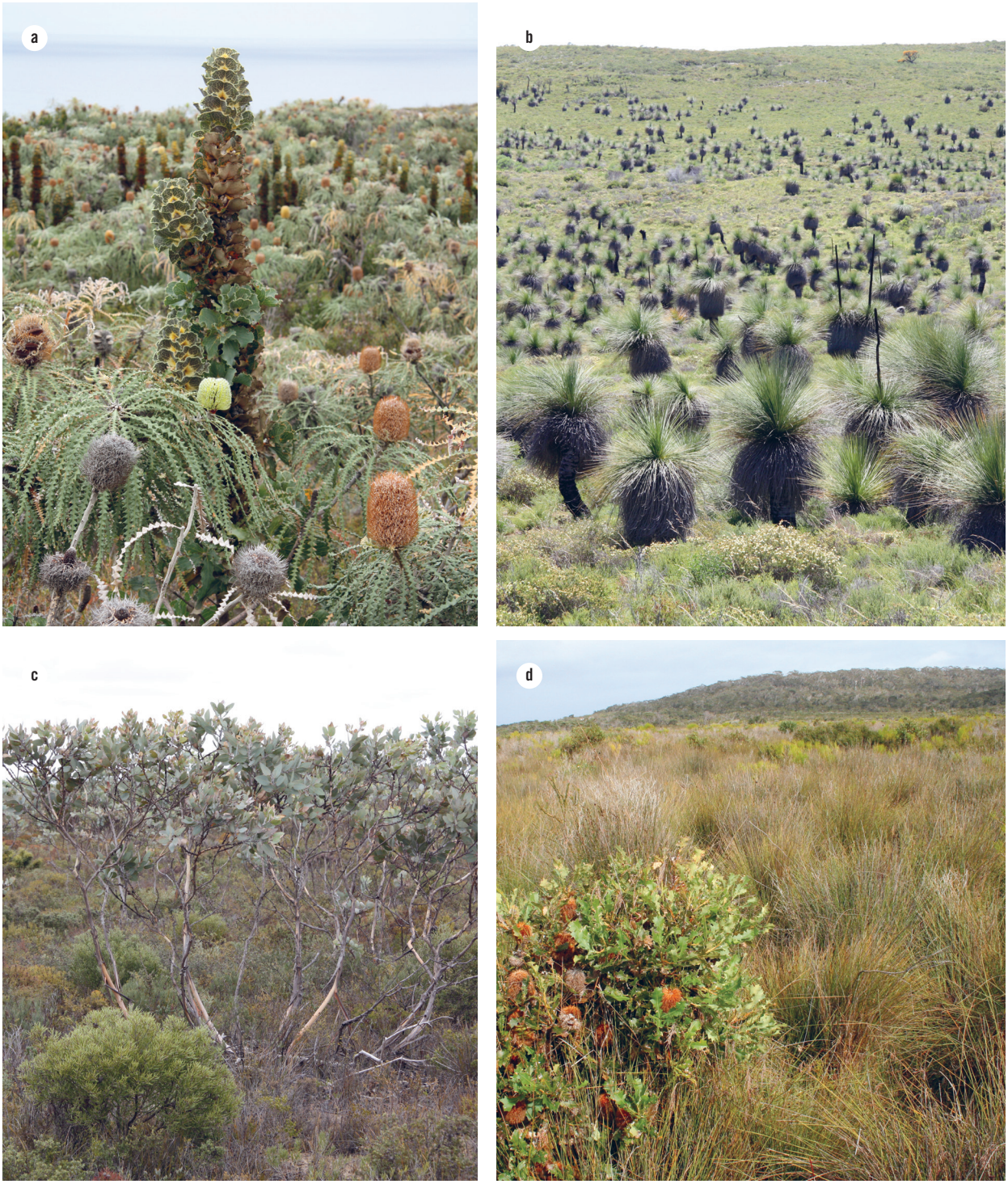


Figure 13A. (a) Myrtaceous-proteaceous kwongan (*Hakea victoria*, *Protea speciosa*), Fitzgerald River National Park. (b) Grasstree kwongan (*Xanthorrhoea preissii*), Wanagarren Nature Reserve, north of Lancelin. (c) Myrtaceous-proteaceous kwongan (mallee-heath form) with prominent *Eucalyptus pleurocarpa* (*Eucalyptus tetragona)*, Fitzgerald River National Park. (d) Sedge kwongan with Cyperaceae and Anathriaceae, with prominent *Banksia quercifolia*, Walpole-Nornalup National Park, Denmark. Photos: Ladislav Mucina.





Figure 13B. (a): *Banksia* woodland, Moore River National Park, near Orange Springs, with *Banksia attenuata* and *Verticordia nitens* (Myrtaceae) in undergrowth. (b) Wodjil thicket with *Acacia* spp. on Sanford Rock, north of Westonia. (c) Sand kwongan on a dune crest with *Verticordia forrestii* and *Verticordia* sp., northeast of Carnarvon in the Eremaea Region. (d) Coastal shrubland with *Olearia axillaris* on granite, near Augusta. Photos: Ladislav Mucina.


Figure 14A. (a) Laterite kwongan, Payner Road Reserve west of Mogumber. (b) Calcrete kwongan with dominating *Melaleuca huegelii* and *Melaleuca systena*, south of Cervantes. (c) Bassendean sand kwongan with prominent *Conospermum stoechadis*, Moore River National Park, Brand Highway. (d) Granite kwongan at the base of Frenchman Peak, the Cape Le Grand National Park near Esperance. Photos: Ladislav Mucina.

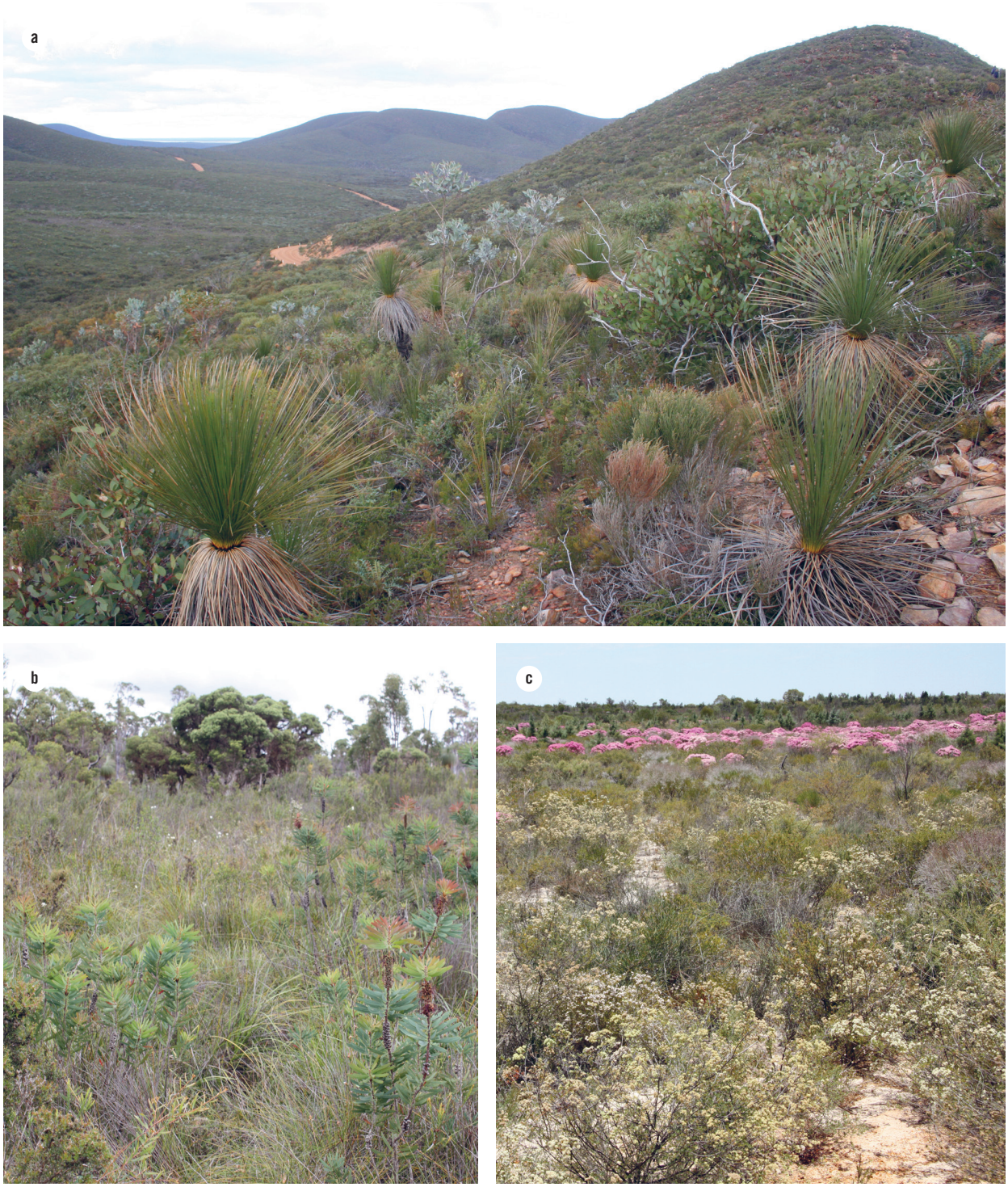


Figure 14B. (a) Stirling sandstone kwongan, Stirling Range National Park, north of Albany. (b) Swamp kwongan, Pingerup Plains near Walpole. (c) Tumblagooda sandstone kwongan with prominent (pink) *Verticordia monadelpha* var. *callitricha*, Kalbarri National Park. Photos: Ladislav Mucina.

resprouting *Eucalyptus* species (possessing huge lignotubers). Mallee is typical of texture-contrast soils and is geographically (and possibly also vegetation-dynamically) linked to the eucalypt-dominated semi-arid woodlands. Wodjil, on the other hand, is dominated by reseeding species of *Acacia*, *Hakea*, *Grevillea* and *Allocasuarina* as well as some *Eucalyptus*. Wodjil is especially typical for flat rolling landscapes on granite-derived coarse sands. The soils are known to be sandy (often deep), acidic and somewhat nutrient-richer than those supporting the sand and laterite kwongan heath. Communities of the wodjil thickets have been described (under various names) from the wheatbelt (*e.g.*, Beard, 1972; Keighery *et al.*, 2002: 'granite heath 7a'; Gibson *et al.*, 2004, *e.g.*, 'Group 16') and other regions of south-western Australia (see Beard's 1:250,000 map series and Fig. 12).

There are not many concrete field data available on wodjil and none have been classified to formalise the vegetation typology. Informally, it could be possible to classify the wodjil on the basis of the nutrient status of soils and the regional climate; however, at this stage we refrain from attempting such classification as it is should be clarified to which extent similar thickets found on Banded Iron Formation outcrops and the Greenstone belt outcrops belong to this group. For the latter, data are available in numerous vegetation surveys (Newbey *et al.*, 1995; Gibson & Lyons, 1998a, b, 2001a, b; Newbey & Hnatiuk 1998; Gibson, 2004a, b; Gibson *et al.*, 2007; Meissner & Caruso, 2008a, b).

### On coastal dune and cliff scrub

The coastal scrub on mobile and/or partly stabilised Spearwood dunes, dominated by *Scaevola* (Goodeniaceae), *Olearia* (Asteraceae), *Myoporum* (Myoporaceae), *Acacia* (Fabaceae) and associated graminoids such as *Lepidospermum* (Cyperaceae) and *Spinifex* (Poaceae) and many perennial and annual herbs, does not qualify as kwongan. This vegetation is structurally analogous to the Cape Western Strandveld thickets (Rebelo *et al.*, 2006, pp. 197–207). Yet, unlike the South African strandveld, these coastal thickets typical of Australian seaboards are not (as a rule) fire-shy (Milewski, 2002).

In principle, we do not consider the coastal thickets (often dominated by asteraceous, goodeniaceous and myoporaceous scrub of the front dunes and wind-sheered scrub on coastal cliffs and headlands (Fig. 14) as 'kwongan'. They are new assembly creations occupying young (YODFEL; Hopper 2009) habitats and can be extremely prone to invasions of alien flora.

## FUTURE CHALLENGES: NEW GOALS OF BIOGEOGRAPHY IN WESTERN AUSTRALIA

Despite the significant progress in biodiversity survey in Western Australia (Keighery *et al.*, 2007), floristic data acquisition, storing and in improved access of the data to the public (DPaW, 2013: FloraBase: (http://florabase.dpaw.wa.gov.au/)) and NatureMap (http://naturemap.dec.wa.gov.au) the biogeographic delimitation of the SWAFR as well as its global biogeographic position remain contentious. In particular, the position of the Interzone is in need of clarification. New methodologies (*e.g.*, Kreft & Jetz, 2010; Linder *et al.,* 2012) are offering promising analytical tools. We suggest that it is time to get over using the coincidence of distribution areas of sole species, without considering serious ecological drivers of plant community assembly, as the major criterion of biogeographic regionalisation. It is time to depart from counts of endemics and concentrate on evolutionary assembly as the leading theme of the

biogeographic land classifications. The accumulation of molecular phylogenies, phylogeographic data sets and development of the new generation sequencing, whole-genome screening, gene bar-coding and phylogeographic modelling are yielding extensive new data sets and forcing new ways of thinking about biogeographic divisions of land. Nowhere else in the world is the progress in genomics more exciting than in old stable landscapes of Southern Hemisphere (including the SWAFR) housing one of the species-richest temperate vegetation type – the kwongan shrublands.

The biological survey of Western Australia is far from over. The fact that more than 1000 recognised taxonomic plant entities carry only 'phrase names' (chapter 8) emphasises a need for intensification of taxonomic studies in the State and in SWAFR in particular. Despite all progress in the field of evolutionary plant systematics, Western Australia is still a country in alpha-phase of taxonomic research and building a broad basis for taxonomic work leading to publication of a State-wide Flora should be a priority.

We still know relatively little about the drivers of alpha and beta diversity in kwongan. With regard to alpha diversity, we suggest that further progress will be made by assessing the relative importance of different drivers, instead of searching for single causes (Laliberté *et al.*, 2013). Moreover, the role of soil biota (particularly root pathogens and mutualists) as a potential driver of species coexistence (*e.g.*, de Kroon *et al.*, 2012) deserves to be further explored. Finally, we suggest that approaches based on functional traits (*e.g.*, Shipley *et al.*, 2006) could help to better understand and predict variation in plant community composition along environmental gradients (*e.g.*, soil resource availability) in kwongan.

Where should Western Australia classification and mapping of vegetation go from here? Horizons are wide and the tasks daunting: the standards of the vegetation field survey are in a need of serious updating. The vegetation-structural maps of John S. Beard are out-dated in terms of mapping tools, precision, and especially of concepts. Until recently (Mucina & Daniel, 2013), there have been no broad-scale mapping protocols, and lack of protocols on fine scales (on which most of the current environmental consulting work is performed) is very painful. Western Australia does not enjoy the advantage of having unified and formal system of habitats – a tool that proved to be of indispensable value to nature management (including biodiversity conservation) for instance in Europe (EUNIS: Moss & Davies, 2002; Rodwell *et al.*, 2002; Davies *et al.*, 2004). A quick check of the global facility collating information on major vegetation (mainly plot-based) databases called Global Index of Vegetation-Plot Databases (Dengler *et al.*, 2011; www.givd.info) suggests that Western Australia does not exist. We surmise that the major problem of the vegetation survey in the State is a notorious lack of vegetation plot data to attempt any serious flora-based or plant-functional type-based vegetation classification system. On a conceptual level, the principles of zonality/azonality rather than structural (physiognomic) vegetation complexity should be applied to classify the large-scale vegetation patterns of Western Australia. At finer scales the principles of total floristic composition underpinned by knowledge on the plant community-assembly processes should serve as leading vegetation classification and mapping principles.

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